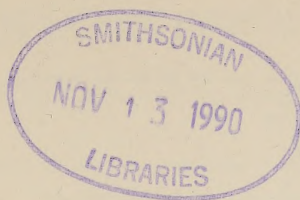




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# ANNALS

## OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN





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- FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627–634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17 (4): 1–51.
- THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

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BENTHIC COMMUNITIES AND  
SEDIMENTARY FACIES IN THE  
LOWER WITTEBERG GROUP  
(DEVONIAN, SOUTH AFRICA)

By  
NORTON HILLER

Cape Town

Kaapstad

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# BENTHIC COMMUNITIES AND SEDIMENTARY FACIES IN THE LOWER WITTEBERG GROUP (DEVONIAN, SOUTH AFRICA)

By

NORTON HILLER

*Department of Geology, Rhodes University, Grahamstown, South Africa*

(With 10 figures)

[Paper presented at the Palaeontological Society of southern Africa Symposium, Cape Town, September 1986]

## ABSTRACT

Rare, Middle–Upper Devonian invertebrate fossils are recorded from a few scattered localities in the lower part of the Witteberg Group. The specimens represent a number of shallow-water communities similar to those recognized in Silurian and Devonian rocks from other parts of the world.

At a single locality near the top of the Weltevrede Formation near Grahamstown, four co-existing communities are recognized: a linguloid–orbiculoid community, a *Tropidoleptus* community, a homalonotid–*Plectonotus* community, and a community of largely infaunal bivalves. Such an assemblage is interpreted as representing the restrictive conditions of an intertidal flat environment.

Analysis of the sedimentary facies shows that the fossils come from a sequence of interbedded shales, siltstones and sandstones arranged in a number of thin upward-fining cycles and displaying flaser, lenticular and wavy bedding. This sequence rests on lithic arenites at the top of an upward-coarsening unit and is overlain by thick cross-bedded quartz arenites of the Witpoort Formation. The top part of the Weltevrede Formation is interpreted as having formed in back-barrier tidal flats during transgressive reworking of a delta top.

In the Western Cape, two localities in the Wagen Drift Formation have yielded a number of brachiopods, including *Tropidoleptus*, *Australospirifer*, chonetaceans and linguloids, as well as bivalves and possible bryozoa. The greater diversity of this brachiopod assemblage suggests somewhat deeper water than the Weltevrede Formation assemblage, probably subtidal. The sedimentary facies of the Wagen Drift Formation are interpreted as having formed in a delta slope environment. The different interpretations of the faunal assemblages from the two areas accord well with the different interpretations of the containing sedimentary facies.

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## INTRODUCTION

The Witteberg Group, topmost division of the tripartite Cape Supergroup, is not noted for its invertebrate fossils, although its plant fossils (Plumstead 1967, 1969) and fish fossils (Jubb 1965; Gardiner 1969) are fairly well documented. However, rare marine invertebrates have been recovered from a number of widely spaced localities in the lower part of the group (Fig. 1). Swart (1950) recorded the presence of the inarticulate brachiopod *Lingula* and further indeterminate brachiopods and bivalves in the lowest part of the Witteberg Group in the Wuppertal area. D. K. Toerien (pers. comm. 1978) recalled finding brachiopods and trilobites in Witteberg shales at Howison's Poort, near Grahamstown, some forty years ago. Theron (1962) described moulds of the nautiloid *Orthoceras* and what are possibly bivalve impressions, along with trace fossils, in rocks of the lower Witteberg Group in the Willowmore district. Look (1967) reported the discovery of a '*Chonetes*' (brachiopod) in sandstones in the lower divisions of the Witteberg Group near Robertson. Hiller & Dunlevey (1978) recorded brachiopods, bivalves and possible bryozoa from one of several localities in the basal unit of the Witteberg Group in the vicinity of Touws River. Theron (1970, 1972), who had also collected in the Touws River area, used brachiopods and a trilobite as a basis for assigning a Lower to Middle Devonian or possibly an Upper Devonian to Lower Carboniferous age to the basal Witteberg beds.

The purpose of the present study was to re-investigate some of the localities, in particular those near Grahamstown in the Eastern Cape and near Touws River in the Western Cape, to see if it was possible to recognize any of the benthic communities that have been described from Silurian and Devonian rocks from other parts of the world, and to see if the environmental information provided by the fossil record was consistent with proposed environmental interpretations

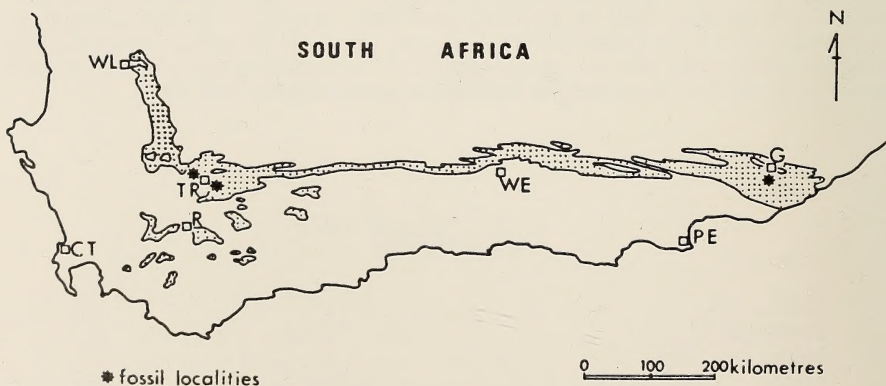


Fig. 1. Map of the major outcrop areas of the Witteberg Group showing the fossil localities. CT—Cape Town, G—Grahamstown, PE—Port Elizabeth, R—Robertson, TR—Touws River, WE—Willowmore, WL—Wuppertal.



based on sedimentary facies analysis. Pickerill & Hurst (1983) have pointed out that the major drawback with many studies that have used fossils to define depth-associated communities, is that they have lacked complimentary facies analysis that could provide corroborative evidence for the environmental assumptions.

### STRATIGRAPHY

In the Western Cape, the Wagen Drift Formation is the lowest unit of the Witteberg Group (Fig. 2). It consists essentially of siltstone and shale with interbedded sandstones. Hiller & Dunlevey (1978), working in the Touws River–Montagu area, subdivided that part of the stratigraphy straddling the Bokkeveld Group–Witteberg Group boundary into three formations, of which the upper two were placed in the Witteberg Group. The South African Committee for Stratigraphy (SACS) (1980) regarded these two units as being informal members within their Wagen Drift Formation. The lower, Nougaspoot Member, consists of dirty white, red-weathering, unevenly bedded, quartz arenites separated by thin beds of laminated siltstone. The sandstones show occasional cross-bedding and contain numerous examples of the trace fossil *Zoophycos* (*Spirophyton*). The upper, Byenest Krans Member, comprises micaceous pale grey to white mudstones and thin, medium-grained sandstones, with red siltstone becoming more common towards the top of the unit. In the middle is a thin, cross-bedded, quartz arenite with *Zoophycos* traces. The Byenest Krans Member

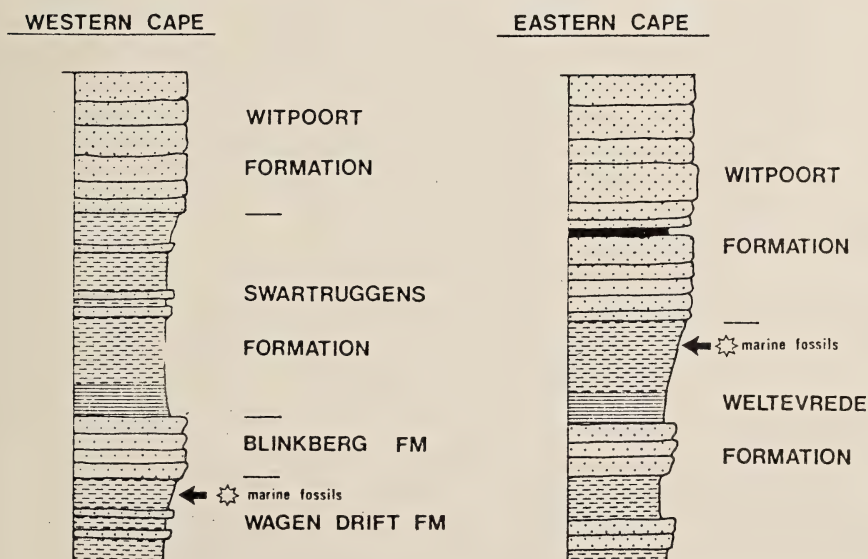


Fig. 2. Stratigraphic columns for the lower part of the Witteberg Group in the Eastern and Western Cape.

has yielded marine invertebrate fossils from three localities in the vicinity of Touws River (Boucot *et al.* 1983).

Overlying the Wagen Drift Formation is the Blinkberg Formation, an extremely mature quartz arenite unit, which contains some plant fossils. This in turn, is overlain by the Swartruggens Formation, a relatively thick heterolithic unit comprising siltstone and shale with thin sandstone interbeds, and containing plant fossils and *Zoophycos* traces. The top of the Weltevrede Subgroup is occupied by the Witpoort Formation, a thick sequence of white-weathering quartz arenites with thin shale partings and containing plant fossils.

In the Eastern Cape the lateral equivalent of the Wagen Drift, Blinkberg and Swartruggens formations is the Weltevrede Formation (Fig. 2). It is a thick succession of shales and siltstones with substantial quartz arenite units, two of which have been accorded member status. At the base of the formation the Driekuilen Sandstone Member occupies much the same position as the Nougaspoot Member does in the west, and near the middle of the formation is the Blinkberg Sandstone Member (SACS 1980). Plant fossils and trace fossils, including burrows, tracks and trails of various kinds, as well as *Zoophycos*, have been found throughout the Weltevrede Formation, whereas the uppermost part has yielded marine invertebrates. Overlying the Weltevrede Formation, the Witpoort Formation again consists of thick cross-bedded quartz arenites and thin carbonaceous shales. Plant fossils and trace fossils have been recorded.

### SEDIMENTARY FACIES

In their summary of the depositional environments, Tankard *et al.* (1982) stated that the sedimentation in the lower part of the Witteberg Group was controlled by the continuation of a series of transgressions and regressions that was established earlier in the Bokkeveld times. The lithofacies are relatively sandy and similar to those of the Bokkeveld Group, which have been interpreted as being the deposits of arcuate deltas subject to marine reworking similar to the present-day Brazos River delta of Texas and the São Francisco delta of Brazil (Tankard & Barwis 1982).

Analysis of the sedimentary facies exposed in Howison's Poort, near Grahamstown (Fig. 3), shows that the upper part of the Weltevrede Formation displays two distinct facies associations. A lower upward-coarsening sequence consists of interbedded micaceous shales and siltstones displaying lenticular bedding, passing upward into horizontally laminated and ripple cross-laminated sandstones (Fig. 4). Load structures are a feature of several sandstone-shale contacts. This sequence is interpreted as the product of a prograding distributary mouth bar in a delta complex (Wright 1978). It is overlain by a thin (2 m) upward-fining sequence that shows ripple cross-laminated sandstone with flaser bedding at its base, passing upward gradually into shale. Interpretation of this sequence is made difficult by the fact that it is abruptly truncated by a major erosion surface, but it is thought to be part of an inter-distributary bay fill (Elliot 1974).



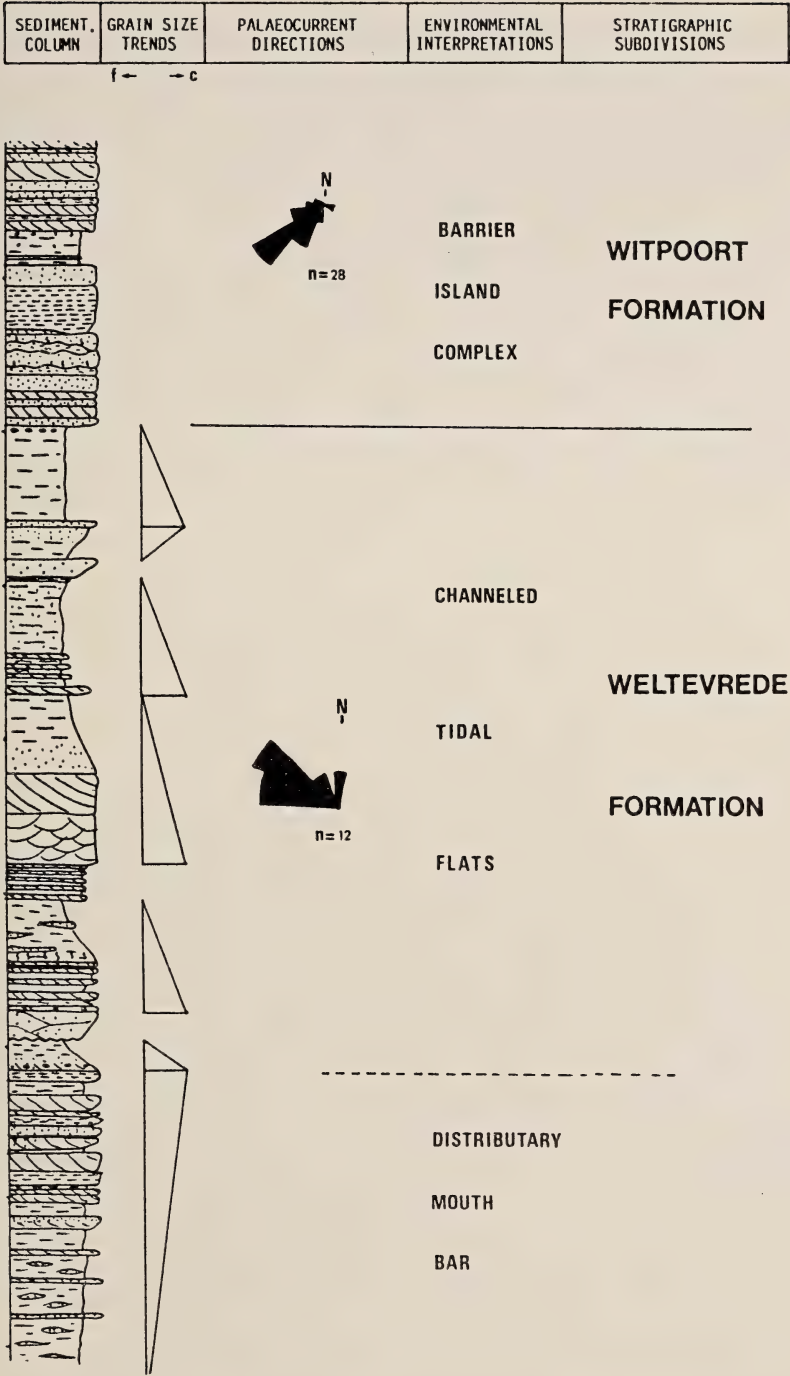


Fig. 3. Stratigraphic log of about 100 m of strata in Howison's Poort, near Grahamstown.



Fig. 4. Top of an upward-coursening sequence in the Weltevrede Formation, Howison's Poort.

The major erosion surface marks the end of the constructional phase of delta out-building and the remaining sediments of the Weltevrede Formation were deposited during a destructional phase. This involved transgressive marine reworking of the delta top (Fisher *et al.* 1969). The upper 70 m of the Weltevrede Formation comprise quartz arenites, siltstones and shales arranged in a number of upward-fining cycles (Fig. 5). The sandstone units thin upwards and are overlain by vertical alternations of siltstone and shale in which flaser and lenticular bedding are common. Trace fossils are common throughout the sequence and marine invertebrates were recovered from the topmost cycle. The upward-fining cycles are interpreted as being the products of a tidal-flat environment crossed by meandering tidal channels (Tankard & Barwis 1982).

The change-over from the Weltevrede Formation to the Witpoort Formation is thought to mark a major change in shoreline configuration from a lobate or arcuate deltaic shoreline to a linear barrier-beach shoreline (Johnson 1976). This change must reflect a reduction in the sediment supply to the shore zone and a decrease in the rate of subsidence so that marginal marine processes rework and redistribute the sediment along the shore. Wave reworking of delta front sands under transgressive conditions produced barrier islands that migrated landwards over the tidal-flat facies.

The Witpoort Formation consists mostly of mature sandstones. In the basal 10–12 m these are brownish in colour, fine to medium grained, and display horizontal lamination and ripple cross-lamination. Above this level the sandstones are cleaner, slightly coarser grained, greyish quartz arenites displaying planar and trough cross-bedding and horizontal lamination. The lowest sand-





Fig. 5. Thin upward-fining sequence near the top of the Weltevrede Formation, Howison's Poort.

stones were probably deposited by wash-over processes into the tidal-flat area. Reinson (1984) has noted that wash-over is one of the main processes by which barrier islands migrate landward and that scouring associated with wash-over is responsible for the initiation of new tidal inlets. The clean quartz arenites that form the bulk of the Witpoort Formation show many of the characteristics of tidal-inlet channel fill, tidal deltas, and beach and foreshore deposits similar to



Fig. 6. Black carbonaceous shale of lagoonal origin, overlain and underlain by barrier island sandstones, Witpoort Formation, Howison's Poort.

those described from various modern environments (e.g. Kumar & Sanders 1974; Hubbard & Barwis 1976; Reddering 1983). The quartz arenite sequence is interrupted by the development of thin (1 m thick) dark grey to black carbonaceous shales with silty layers, siderite nodules and numerous plant fragments. These probably formed in stagnant back-barrier lagoonal or marsh environments (Fig. 6).

A similar detailed facies analysis is not available for the lower part of the Witteberg Group in the Western Cape but Theron (1970) stated that the basal Witteberg beds are part of a regressive cycle that follows directly on from similar cycles in the Bokkeveld Group. Tankard *et al.* (1982) indicated that the Wagen Drift Formation represents the subaqueous portion of a delta and that the overlying quartz arenites of the Blinkberg Formation are the products of reworking of the delta, much the same as Tankard & Barwis (1982) described from the Bokkeveld Group.

## FAUNA

The two localities within the Wagen Drift Formation near Touws River, from which material was collected for this study, have yielded an inarticulate brachiopod (Fig. 7E), several articulate brachiopods (Fig. 7D), bivalves and possible bryozoa. Generally, the preservation of the specimens is rather poor and identification beyond generic level is very difficult. The inarticulate brachiopod belongs to the family Lingulidae and specimens in the British Museum (Natural History) have been identified as *Lingula lepta* Clarke, aff. *Trigonoglossa*, and cf. *Barroisella*. The specimens in the author's collection are certainly not *Trigonoglossa*, which has a distinctive ornament, and of the other two identifications *Lingula lepta* seems the more likely. This is a Brazilian species, which is also known from the Bokkeveld Group (Reed 1925). Copper (1977), writing about the Devonian faunas of Brazil, included the species in *Dignomia*, presumably on the basis of its relatively large size and thin shell.

Among the articulate brachiopods *Australospirifer antarctica* (Morris & Sharpe), *Chonetes* sp. and *Tropidoleptus* sp. have been recognized (Boucot *et al.* 1983). The first of these is well known from the Bokkeveld Group and its Falkland Islands and South American correlatives. The bivalves are too poorly preserved for even generic identification.

The assemblage is dominated by brachiopods but their distribution varies within the formation. The articulate brachiopods come from the middle of the unit but recent collecting near the top, just below the junction with the overlying Blinkberg Formation, yielded only specimens of *Lingula lepta*.

The Howison's Poort locality has yielded inarticulate brachiopods, an articulate brachiopod, a homalonotid trilobite, several genera of bivalves, and a bellerophonitid gastropod (Figs 7A–C, 8). The brachiopods include a species of *Lingula*, *Orbiculoidea baini* (Sharpe), which is known from the Bokkeveld Group, the Falkland Islands and Brazil, and the articulate brachiopod



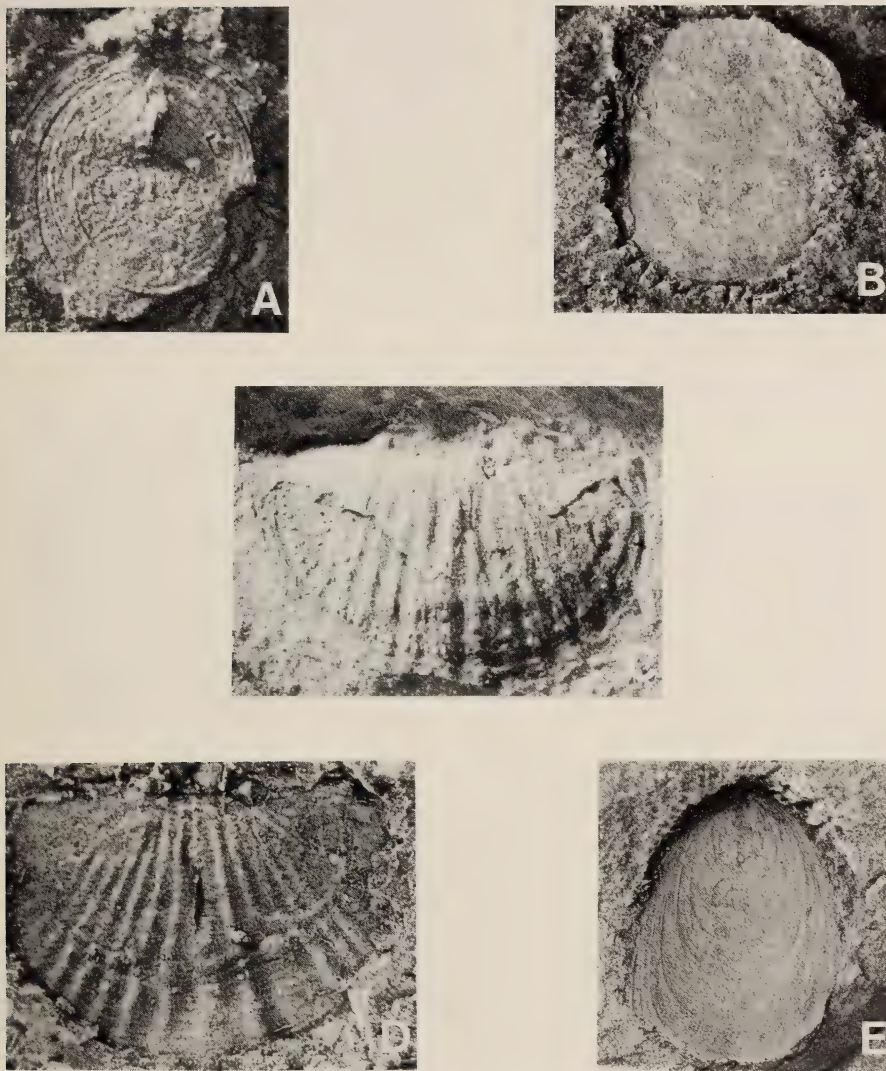


Fig. 7. Brachiopods from the Witteberg Group. A. External mould of a pedicle valve of *Orbiculoidea* sp., Weltevrede Formation, Howison's Poort.  $\times 4$ . B. External mould of a pedicle valve of *Lingula* sp., Weltevrede Formation, Howison's Poort.  $\times 2,5$ . C. Internal mould of a brachial valve of *Tropidoleptus* sp., Weltevrede Formation, Howison's Poort.  $\times 4$ . D. External mould of a brachial valve of *Tropidoleptus* sp., Wagen Drift Formation, Avondrus, south-east of Touws River.  $\times 5$ . E. External mould of a pedicle valve of *Lingula* sp., Wagen Drift Formation, Elim, west of Touws River.  $\times 2,5$ .

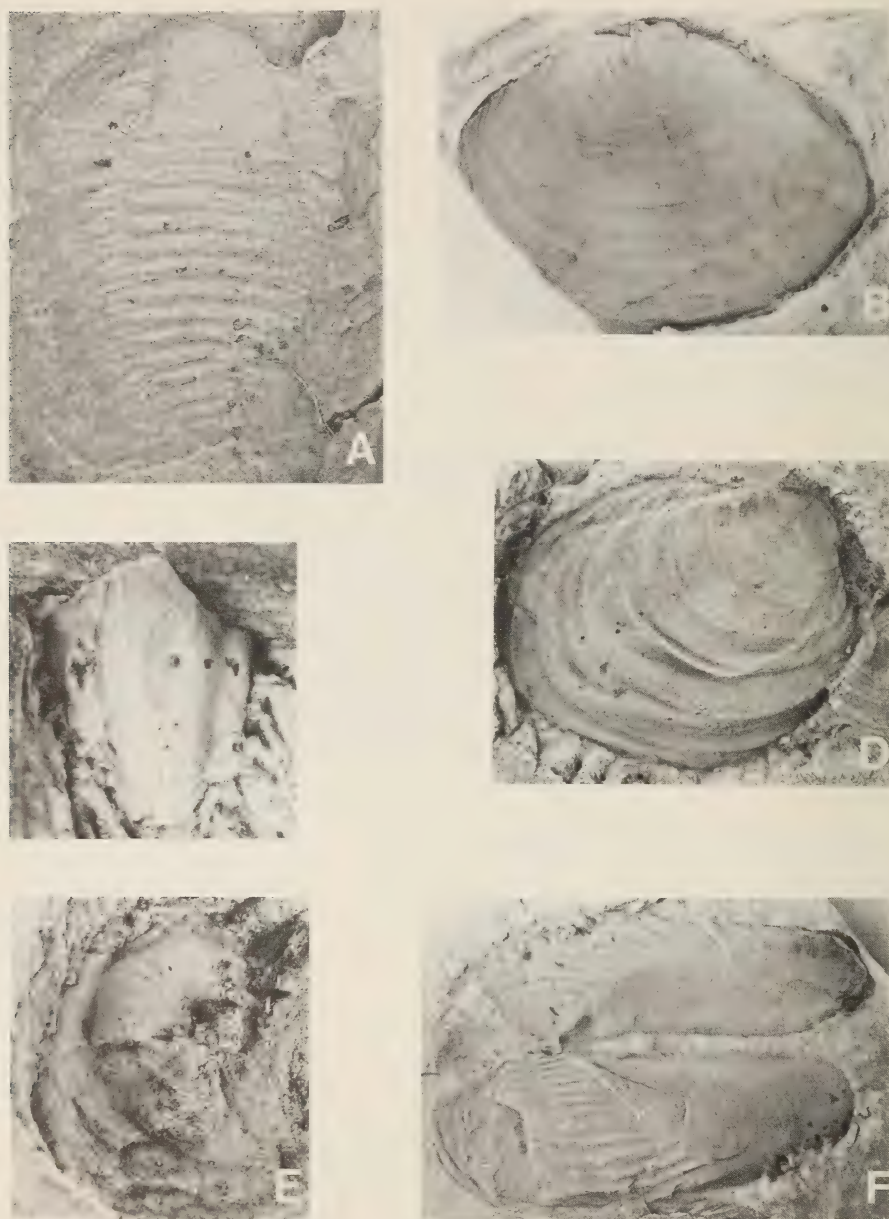


Fig. 8. Fossils from the Weltevrede Formation, Howison's Poort. A. Trilobite, *Trimerus?* sp.  $\times 4$ . B. Bivalve, *Palaeoneilo* sp.  $\times 2$ . C. Gastropod, *Plectonotus* sp.  $\times 4$ . D. Bivalve *Modiomorpha?* sp.  $\times 3,5$ . E. Gastropod, *Plectonotus* sp.  $\times 4$ . F. Bivalve, *Sanguinolites* sp.  $\times 2,5$ . All specimens are preserved as internal moulds.



*Tropidoleptus* sp. A specimen in the British Museum (Natural History) has been identified as aff. *Trigonoglossa* but again nothing in the author's collection corresponds to such an assignment. The generic placement of the trilobite remains in some doubt but workers at the British Museum (Natural History) believe that it might be a species of *Trimerus* (pers. comm. 1986). Among the bivalves the following genera are tentatively recorded: *Palaeoneilo* sp., *Nuculites* sp., *Sanguinolites* sp., *Paraprothyris* sp., *Janeia* sp., and *Modiomorpha* sp. The collection is thus dominated by bivalves. The single gastropod is a species of *Plectonotus*.

### PALAEOECOLOGY

Brachiopods are epifaunal suspension feeders that are restricted to more or less normal marine conditions. The only known exception to this general rule is *Lingula*, which is an infaunal suspension feeder known to be moderately euryhaline and capable of withstanding reduced salinities for short periods. Hammond (1983) showed that a living species of *Lingula* may tolerate salinity levels down to 16‰ and up to 50‰ for prolonged periods, and exposure to levels as low as 5‰ for shorter periods. At the present time the genus lives in nearshore habitats, including estuaries and intertidal flats, often in brackish water, and there is a wealth of evidence to suggest that throughout its stratigraphic range (at least back to the Ordovician), it occurred in nearshore faunas that were characterized by low species diversity usually with no more than five taxa (Raup & Stanley 1971: 208). It seems reasonable to suggest, therefore, that abundant *Lingula* in the Witteberg Group represents a nearshore setting, possibly with fluctuating salinity. However, the greater diversity of brachiopods in the Touws River localities would indicate less stressful salinity conditions. *Orbiculoidea* may have been planktonic or, more likely, epiplanktonic—attaching to algal fronds that are not preserved. Such a life-style would mean that it could turn up in almost any shallow marine habitat but the association of orbiculoid and linguloid brachiopods is a common one in many Silurian and Devonian rocks of nearshore origin (Boucot 1975).

Palaeozoic bivalves were largely non-siphonate and most were shallow infaunal deposit feeders or semi-infaunal suspension feeders (Stanley 1968). In Silurian and Devonian rocks they are commonly associated with *Lingula* in shallow nearshore habitats, although they did range into deeper shelf waters (Copper 1977).

Another common association in Silurian and Devonian rocks is that of homalonotid trilobites with the snail *Plectonotus*, and Boucot (1975) has documented this association from many parts of the world. It is not certain what sort of life habits were adopted by these creatures but the shape of the cephalon on the trilobites suggests they may have foraged for food by ploughing through the upper centimetre or so of sediment. The gastropods may have been herbivores. Homalonotids are known to occur in deeper-water environments, but the

association with *Plectonotus* always seems to occur in a shallow nearshore setting (Boucot 1975).

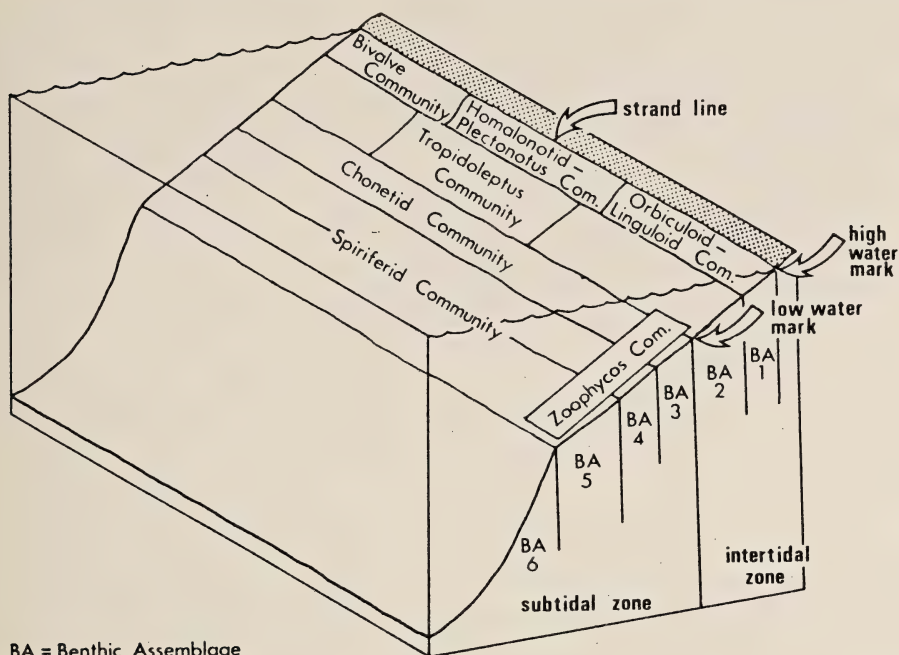
Associations of this sort just described were termed communities by Boucot (1975), who defined a community as a recurring association of taxa that require the same range of environmental conditions or that are dependent on one another. Using a number of such Palaeozoic communities, based largely on brachiopods, he recognized six benthic assemblages representing increasing distance from the shoreline. This, in turn, could be broadly correlated with increasing depth and decreasing temperature. Each benthic assemblage was made up of one or more co-existing communities.

Benthic assemblages 1 and 2 are interpreted as representing the high and low intertidal zones respectively (Boucot 1975); benthic assemblages 3, 4 and 5 represent increasingly deep subtidal areas on the continental shelf, and benthic assemblage 6 represents deeper water beyond the local shelf edge. For the Malvinokaffric Realm (a Silurian–Devonian palaeogeographic and biogeographic realm that included South Africa, the Falkland Islands and South America south of about 10° S), Boucot (1975: 18) showed that benthic assemblage 1 contains three low-diversity communities—a homalonotid–*Plectonotus* community, an orbiculoid–linguloid community and an infaunal bivalve community. Benthic assemblage 2 contains a number of low-diversity brachiopod communities including a *Tropidoleptus* community. Benthic assemblage 3 contains a high-diversity chonetid community, and a high-diversity spiriferid community stretches across benthic assemblages 4 and 5. The trace fossil *Zoophycos* is said to range through benthic assemblages 3–5. Figure 9 provides a summary of this scheme. A certain amount of community mixing may occur at assemblage boundaries.

The low diversity communities, such as are found in benthic assemblages 1 and 2, can be explained by the restrictive conditions of the intertidal environment with its wide fluctuations in temperature, salinity and exposure to the atmosphere. The more stable infaunal environment permits a somewhat more diverse bivalve fauna to be present. The taxa that dominate the low-diversity communities of benthic assemblages 1 and 2 may also be found in high-diversity communities in deeper-water subtidal conditions (Boucot *et al.* 1983).

The collection of fossils from the Howison's Poort locality clearly relate to benthic assemblages 1 and 2 of Boucot's scheme, and can readily be assigned to the four communities making up those assemblages. This would suggest that the fossils represent an intertidal environment. Figure 10 is a cartoon reconstruction of the environment envisaged for the Howison's Poort site. In contrast, the brachiopod fauna from the Western Cape localities would indicate the deeper-water subtidal conditions of benthic assemblages 3 and 4, although the number of *Lingula* specimens recovered from the top of the Wagen Drift Formation might suggest a progressive shallowing of the environment.





BA = Benthic Assemblage

Fig. 9. Schematic representation of the communities and benthic assemblages recognized in the Witteberg Group, showing their relationship to depth and distance from the shore line. (After Boucot 1975.)

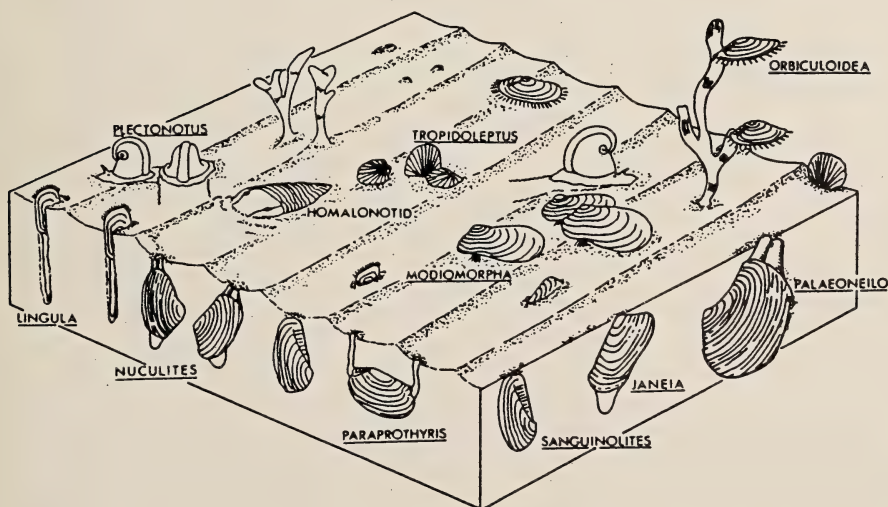


Fig. 10. Cartoon reconstruction of the intertidal communities of the Weltevrede Formation in Howison's Poort.

## AGE

The general lack of fossils in the Witteberg Group has made dating of the rocks rather difficult. Fish remains from the Waaipoort Formation in the upper part of the group led Gardiner (1969) to propose a Lower Carboniferous age, whereas Stapleton (1977a, 1977b) used spores from the same horizon to determine a Middle or Upper Devonian (Givetian–Frasnian) age. Witteberg plant macrofossils suggested a late Devonian age to Plumstead (1967, 1969). Boucot *et al.* (1983) discussed these various age determinations and used the presence of the brachiopod *Tropidoleptus*, a genus that apparently does not occur in similar facies in the underlying Bokkeveld Group, to suggest a Givetian or Frasnian age for the lower part of the Witteberg Group.

Such an age determination agrees well with the suggestion of Cooper (1982, 1986), who used eustatic sea-level changes to effect a correlation with Devonian rocks in Europe and North America. His proposals gave a Givetian age for the Wagen Drift Formation and a Frasnian age for the top part of the Weltevrede Formation. This slight age difference is unimportant in explaining the differences in the fauna between the localities described here. As has been pointed out, many of the forms recovered from these localities are quite long ranging and are found in the Bokkeveld Group. Environmental differences are the important factors in determining the faunal differences.

## CONCLUSIONS

Rare Middle to Upper Devonian marine invertebrates from a few widespread localities in the lower part of the Witteberg Group represent a number of benthic communities similar to those recorded from other parts of the world. The locality at Howison's Poort in the Eastern Cape has yielded an intertidal assemblage dominated by infaunal bivalves but also containing orbiculoid and linguloid inarticulate brachiopods, *Tropidoleptus* (an articulate brachiopod), a homalonotid trilobite and the gastropod *Plectonotus*. In contrast to this, two localities in the Wagen Drift Formation near Touws River have yielded a deeper-water subtidal assemblage dominated by articulate brachiopods, including *Australospirifer*, *Chonetes* and *Tropidoleptus*. Increasing numbers of the inarticulate *Lingula* near the top of the formation may indicate shallowing of the water.

The different interpretations of the faunal assemblages from the two areas accord well with the different interpretations of the containing sedimentary facies. The shales at the top of the Weltevrede Formation at Howison's Poort are thought to have been deposited in intertidal flats established during transgressive reworking of an abandoned delta lobe. The Wagen Drift Formation is taken to represent a prograding delta and its shales were deposited in a delta slope environment.



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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

#### Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierii* Philippi, 1861: 87.

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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NORTON HILLER

BENTHIC COMMUNITIES AND  
SEDIMENTARY FACIES IN THE LOWER  
WITTEBERG GROUP  
(DEVONIAN, SOUTH AFRICA)



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*HATCHERICERAS* STANTON, 1901  
(CEPHALOPODA, AMMONOIDEA),  
FROM THE BARREMIAN OF ZULULAND

By  
WILLIAM JAMES KENNEDY  
&  
HERBERT CHRISTIAN KLINGER

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(With 6 figures)

[MS accepted 27 October 1989]

ABSTRACT

*Hatchericeras patagonense* Stanton, 1901, previously known only from the Austral Basin of Argentina, is described from the Barremian of northern Zululand. All but one described species of *Hatchericeras*, and of *Pseudohatchericeras* Leanza, 1970, are placed in synonymy.

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INTRODUCTION

The genus *Hatchericeras* was introduced by Stanton (1901) for a series of ammonites collected by J. B. Hatcher during the Princeton University expeditions to Patagonia (1896–1899) (see Hatcher 1900) near the mouth of the canyon of the Río Tarde, from what were termed the Belgrano beds, and from essentially the same horizon some 16.5 km (10 miles) east of Lake Pueyrredón, in Patagonia. Stanton dated the fauna as ‘not later than the Gault’ (p. 10), that is to say Albian or older, describing *Hatchericeras patagonense*, the type species, based on three specimens (1901: 38, pl. 8 (figs 1–2), pl. 9 (fig. 1); *H. argentinense* (1901: 39, pl. 9 (figs 2–5)), based on at least four specimens; *H.?* *tardense*

(1901: 41, pl. 10 (figs 3–5)), based on one specimen; and *H.?* *pueyrrydonense* (1901: 42, pl. 10 (figs 1–2)), based again on one specimen only. Stanton was uncertain of the affinities of his new genus, but concluded it was closest to the Hoplitidae (1901: 38). Favre (1908: 631, pl. 35 (figs 3–4), text-fig. 5) introduced a further species, *H. stantoniense*, from the Cerro Belgrano, Patagonia, based on a solitary specimen, without commenting on its taxonomic position. Spath (1923: 307) thought *Hatchericeras* might be matched with his new genus *Proleopoldia*, subsequently referred to the subfamily Garniericeratinae of the Craspeditidae (Perisphinctaceae) with a query by Wright (1957: L344). Roman (1938: 343) referred *Hatchericeras* to the Hauterivian and placed it in the subfamily Neocomitinae of the Perisphinctaceae, a view followed by Wright (1957: L360) and Woods (1962: 240). Leanza (1970: 233) believed *Hatchericeras* was of Albian date, and placed it in the subfamily Gastroplitinae (Hoplitaceae), describing specimens of *H. patagonense*, *H. santacrucense* Leanza, 1970 (p. 237, fig. 32 (1, 2)), *H. semilaeve* Leanza, 1970 (p. 237, figs 33 (1–4), 34 (1, 2), 35 (1, 3), 36 (1), 37 (1, 2)) and *H. hatcheri* Leanza, 1970 (p. 242, fig. 38 (1–3)), and introducing the genus *Pseudohatchericeras* with *H. argentinense* Stanton, 1901, as type species. All appear to come from the same general level in the Río Belgrano Formation, albeit from different localities, according to Leanza.

As Riccardi & Aguirre Urreta (1989: 447) noted, the seeming endemism of *Hatchericeras* and other elements of the Patagonian fauna led to the view that rocks of Valanginian–Barremian age were absent (e.g. Leanza 1963) in the Austral Basin. Subsequently, Riccardi (1984a, 1984b, 1988) and Riccardi & Aguirre Urreta (1989) recognized a Hauterivian to Barremian zonal sequence of:

Barremian	{	<i>Colchidites</i> Zone
	{	<i>Hatchericeras patagonense</i> Zone
Hauterivian	{	<i>Favrella wilckensi</i> Zone
	{	<i>Favrella americana</i> Zone

*Hatchericeras* species are listed only from the *H. patagonense* Zone, which also yields *Cryptocrioceras yrigoyeni* (Leanza, 1970), *Hemihoplites varicostatus* Riccardi & Aguirre Urreta, 1989, and *Sanmartinoceras africanum insignicostatum* Riccardi *et al.*, 1987. The *Colchidites* Zone yields *Colchidites vulanensis* Egoian, 1965 *australis* Klinger, Kakabadze & Kennedy, 1984, *Heteroceras elegans* Rouchadzé, 1933, and *S. africanum insignicostatum*.

All of these species occur in Zululand, where *Sanmartinoceras africanum* Kennedy & Klinger, 1979, is represented by the nominate subspecies rather than *S. africanum insignicostatum*; aconeceratids are described by Kennedy & Klinger (1979); heteroceratids by Klinger (1976), Klinger *et al.* (1984) and Aguirre Urreta & Klinger (1986); *Hatchericeras* herein; and the remaining heteromorphs in a forthcoming publication (Klinger & Kennedy in prep.). The *H. patagonense* Zone corresponds to division Barremian I of Kennedy &



Klinger (1975: 274), and the *Colchidites* Zone to division Barremian II of these authors.

The *Hatchericeras* described below are amongst the oldest ammonites known from Zululand, first appearing in bed 4 at locality 170 on Mlambo-  
ngwenya Spruit (Kennedy & Klinger 1975, fig. 11; Aguirre Urreta & Klinger 1986, fig. 3).

#### LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

OUM Oxford University Museum, Oxford.

PU Princeton University Collections, Princeton.

SAM South African Museum, Cape Town.

#### DIMENSIONS OF SPECIMENS

All dimensions given below are in millimetres: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.

Figures in parentheses are dimensions as a percentage of the total diameter.

#### SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916), as reviewed by Kullman & Wiedmann (1970) is followed here: E = external lobe, L = lateral lobe, U = umbilical lobe, I = internal lobe.

#### SYSTEMATIC PALAEOLOGY

Phylum MOLLUSCA

Class CEPHALOPODA

Order AMMONOIDEA Zittel, 1884

Suborder AMMONITINA Zittel, 1884

Superfamily PERISPINCTACEAE Steinmann, 1890

Family *Neocomitidae* Salfeld, 1921

Subfamily *Neocomitinae* Salfeld, 1921

Genus *Hatchericeras* Stanton, 1901

[= *Pseudohatchericeras* Leanza, 1970]

*Type species.* *Hatchericeras patagonense* Stanton, 1901 (p. 38, pl. 8 (figs 1–2), pl. 9 (fig. 1), by original designation by Stanton (1901: 35).

#### Discussion

*Pseudohatchericeras* Leanza, 1970 (p. 244), with *Hatchericeras argentinense* Stanton, 1901 (p. 39, pl. 9 (figs 2–5) as type species, seems to be no more than a

flat-ribbed *Hatchericeras* (e.g. compare Riccardi 1988, pl. 10 (figs 1–2) and pl. 10 (figs 3–4)), and is regarded as a synonym. Recognition that *Hatchericeras* is Barremian indicates that it is unlikely to be a member of the Albian–Lower Cenomanian Gastroplitinae as proposed by Leanza (1970), whereas the strong similarities of ornament and suture line link it to the Neocomitinae, as proposed by Roman (1938) and Wright (1957). The resemblance of *Hatchericeras* and *Alopecoceras* Kennedy & Klinger, 1978 (type species *Alopecoceras ankeritterae* Kennedy & Klinger, 1978: 60, figs 1–4, 5A–B, 6, 7E–G), from the Middle Albian of Zululand, as suggested by Kennedy & Klinger (1978), is thus revealed as homeomorphous. The origin of *Alopecoceras* is possibly in the ‘*Cleonicer*’-like forms described from the Albian of Madagascar by Collignon (1963).

### Occurrence

Barremian of the Austral Basin, southern Patagonia, and northern Zululand. Woods (1962) recorded *Hatchericeras lakefieldense* from the Laura Basin of Queensland, Australia, and regarded it as Lower Hauterivian, on the basis of the presumed Hauterivian age of the Patagonian examples of *Hatchericeras*.

### *Hatchericeras patagonense* Stanton, 1901

#### Figs 1–6

*Hatchericeras patagonense* Stanton, 1901: 38, pl. 8 (figs 1–2), pl. 9 (fig. 1). Roman, 1938: 343, fig. 34, 323. Wright, 1957: L361, fig. 470 (1). Leanza, 1970: 234, fig. 30 (1–4), fig. 31a (1, 3), fig. 31b (2). Riccardi, 1988, pl. 9 (figs 7–8).

*Hatchericeras argentinense* Stanton, 1901: 39, pl. 9 (figs 2–5).

*Hatchericeras? tardense* Stanton, 1901: 41, pl. 10 (figs 3–5). Riccardi, 1988, pl. 10 (figs 6–7).

*Hatchericeras? pueyrrydonense* Stanton, 1901: 42, pl. 10 (figs 1–2). Riccardi, 1988, pl. 10 (figs 3–4).

*Hatchericeras stantoniense* Stant. n. sp. Favre, 1908: 631, pl. 35 (figs 3–4), text-fig. 5.

*Hatchericeras* cf. *pueyrrydonense* Stant. Favre, 1908: 632.

*Hatchericeras santacruzense* Leanza, 1970: 237, fig. 32 (1–2).

*Hatchericeras semilaeve* Leanza, 1970: 237, fig. 33 (1–4), fig. 34 (1–2), fig. 35 (1–3), fig. 36 (1), fig. 37 (1–2). Kennedy & Klinger, 1978, figs 6C, 7A–D.

*Hatchericeras hatcheri* Leanza, 1970: 242, fig. 38 (1–3).

*Pseudohatchericeras argentinense* (Stanton) Leanza, 1970: 244, fig. 39 (1–3). Riccardi, 1988, pl. 10 (figs 1–2).

### Type

Holotype is PU 66, the original of Stanton (1901, pl. 8 (figs 1–2), pl. 9 (fig. 1)), refigured by Riccardi (1988, pl. 9 (figs 7–8)), from Lago Pueyrredón, Santa Cruz Province, Argentina.

### Material

OUM KX 1804 and 1819, from bed 3 at locality 170 of Kennedy & Klinger (1975), and OUM KX 1820–1821, from a slightly higher horizon, Makatini Formation, Mlambongwenya Spruit, Zululand. Barremian I.

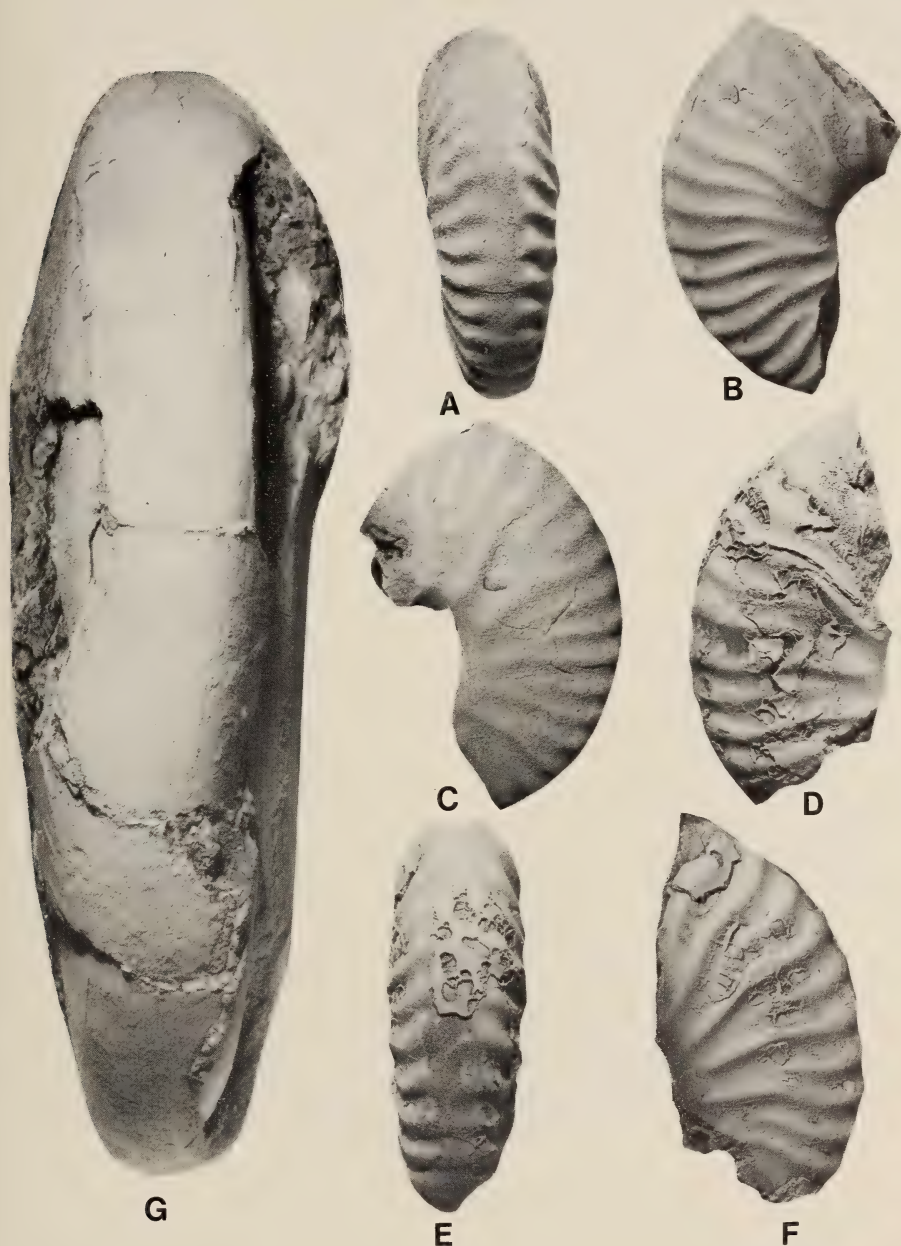


Fig. 1. *Hatchericeras patagonense* Stanton, 1901. A-C. OUM KX 1820.  
D-F. OUM KX 1819. G. OUM KX 1804. A-F  $\times 1$ , G  $\times 0,6$ .



*Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
Holotype 1 <sup>1</sup> PU 66	250 (100)	72 (28,8)	148 (59,2)	0,49	53 (21,2)
Paratype 1 <sup>1</sup>	210 (100)	63 (30,0)	113 (53,8)	0,55	45 (21,4)
Paratype 2 <sup>1</sup>	300 (100)	94 (31,3)	175 (58,3)	0,54	62 (20,7)
OUM KX 1804	250 (100)	72 (28,8)	123 (49,2)	0,58	31 (12,4)
OUM KX 1819		51 (—)	86 (—)	0,59	

<sup>1</sup> —from Stanton (1901)

*Description*

OUM KX 1820 and 1821 (Fig. 1A–F) are fragments of small body chambers of specimens that were an estimated 50–60 mm in diameter. Coiling is involute, with a small, shallow umbilicus. The umbilical wall is flattened and outward-inclined, giving rise to a conical circumumbilical pit. The whorl sections are compressed, with broadly rounded inner flanks, flattened, convergent outer flanks and a somewhat flattened venter in intercostal section, with the greatest breadth just outside the umbilical shoulder. Strong, distant, narrow ribs are straight and prorsiradiate on the inner flank. They flex back and thicken across the mid-flank, where they are convex, flex forwards and are concave on the outer flank, and strengthen into blunt incipient ventrolateral bullae. The ribs weaken somewhat on the venter, where they are broad and transverse. Two ribs intercalate between the primaries, arising either low on the flank or at mid-flank, strengthening to match the primary ribs on outer flank and venter. The dorsum of OUM KX 1820 shows details of the ornament at an even smaller diameter; the ribs are more crowded than in the somewhat larger whorls.

OUM KX 1819 (Figs 3B, 4) is part of an adult phragmocone and the beginning of the body chamber, with a maximum preserved whorl height of 100 mm. Ornament is greatly reduced, with low, broad prorsiradiate ribs (Fig. 4) on the flank, narrowing somewhat towards the umbilicus. The venter is broad, flat and smooth (Fig. 3B). OUM KX 1804 (Figs 1G, 2) is a complete adult, 250 mm in diameter. Ornament on the body chamber is reduced to irregular low ribs and folds on the internal mould; where replaced shell survives, it is covered by delicate prorsiradiate growth lines and striae. The venter is flattened throughout, and broadens towards the adult aperture.

Suture (Fig. 6) with large, asymmetrically subtrifid E/L, broad trifid L, smaller, subtrifid L/U<sub>2</sub> and U<sub>2</sub>.

*Discussion*

The largest South African specimen differs in no significant respect from the holotype of *H. patagonense*, illustrated photographically by Riccardi (1988, pl. 9 (figs 7–8)) or the Argentinian specimen shown in Figures 3A and 5, whereas the type series of *H. semilaeve* Leanza, 1970 (p. 237, fig. 33 (1–4), fig. 34 (1–2), fig. 35 (1–3), fig. 36 (1), fig. 37 (1–2)), link these feebly ornamented adults to



Fig. 2. *Hatchericeras patagonense* Stanton, 1901. OUM KX 1804.  $\times 0,6$ .





Fig. 3. *Hatchericeras patagonense* Stanton, 1901. A. SAM-PC8454, from Chorrillo Rivero-Río Roble, Argentina. B. OUM KX 1819. All  $\times 1$ .





Fig. 4. *Hatchericeras patagonense* Stanton, 1901. OUM KX 1819.  $\times 1$ .



Fig. 5. *Hatchericeras patagonense* Stanton, 1901. SAM-PC8454, from Chorrillo Rivero-Río Roble, Argentina. Specimen kindly donated by M. B. Aguirre Urreta, Buenos Aires.  $\times 1$ .



Fig. 6. *Hatchericeras patagonense* Stanton, 1901. OUM KX 1819. Suture line.  
Scale = 10 mm.

the small specimens illustrated here as Figure 1A–F. The other species described by Stanton (1901), Favre (1908), and Leanza (1970), from a limited stratigraphical interval only, in the authors' view, illustrate no more than the normal range of variation in juvenile ammonites, and are regarded as conspecific. *Hatchericeras lakefeldense* Woods, 1962, is difficult to interpret. It looks like a representative of *Hatchericeras*, but seems more evolute, with a wider umbilicus than the type species, *H. patagonense*, when adult.

#### Occurrence

Barremian, *Hatchericeras patagonense* Zone of the Austral Basin, Argentina, and Makatini Formation, Barremian I, Locality 170, Mlambongwenya Spruit, Zululand.

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Family **Nuculanidae**

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierti* Philippi, 1861: 87.

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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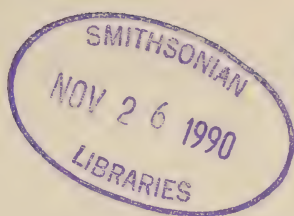
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*HATCHERICERAS* STANTON, 1901  
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FROM THE BARREMIAN OF ZULULAND

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# ANNALS

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(continued inside back cover)

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DEEP-WATER QUATERNARY OSTRACODA  
FROM THE CONTINENTAL MARGIN OFF  
SOUTH-WESTERN AFRICA  
(SE ATLANTIC OCEAN)

By  
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&  
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(With 63 figures and 13 tables)

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ABSTRACT

Thirty-one species of benthic Ostracoda, representing 15 genera and two indeterminate categories, are recorded from water depths greater than 900 m on the continental margin off south-western Africa. Important faunal changes at certain depths allow the assemblages to be grouped into Upper Bathyal, Lower Bathyal and Abyssal zones. The limits of these faunal zones correlate with boundaries within and between the major water masses: the Neritic/Upper Bathyal boundary lies at the bathyal thermocline, which coincides with the base of the salinity minimum zone of the Antarctic Intermediate Water (AAIW) mass (c. 950 m); the Upper/Lower Bathyal boundary lies at the AAIW/North Atlantic Deep Water (NADW) mass contact (1 500 m); and the Lower Bathyal/Abyssal boundary lies at the top of the NADW core zone (c. 2 000 m). These structural changes in the water column are accompanied by alterations in physical and chemical properties, and we attempt to assess the effectiveness of these as barriers that maintain the integrity of the faunal zones. The relationships are complex and vary greatly from species to species. In addition, we find that, although the overall abundance of ostracods on the adjacent continental shelf positively correlates with high mud content in the sediments, this relationship does not hold for continental slope and rise area. Certain deep-water species, however, do prefer fine-grained substrates. In comparison with ostracod faunas from similar depths in other parts of the Atlantic Ocean, the populations off south-western Africa have Lower Bathyal and Abyssal taxa at somewhat shallower levels.

One genus (*Rugocythereis*) and seven species are new: *Krithe capensis*, *K. spatularis*, *K. rex*, *K. peypouqueti*, *Cytheropteron cronini*, *Buntonia rosenfeldi*, and *Echinocythereis whatleyi*. Six species have previously been described: *Rugocythereis horridus* (Whatley & Coles, 1987), *Cytherella serratula* (Brady, 1880), *Dutoitella suhmi* (Brady, 1880), *Abyssocythere australis* Benson, 1971, *Poseidonamicus major* Benson, 1972, and *Henryhowella melobesioides* (Brady, 1869). Fourteen species are left in open nomenclature.

## CONTENTS

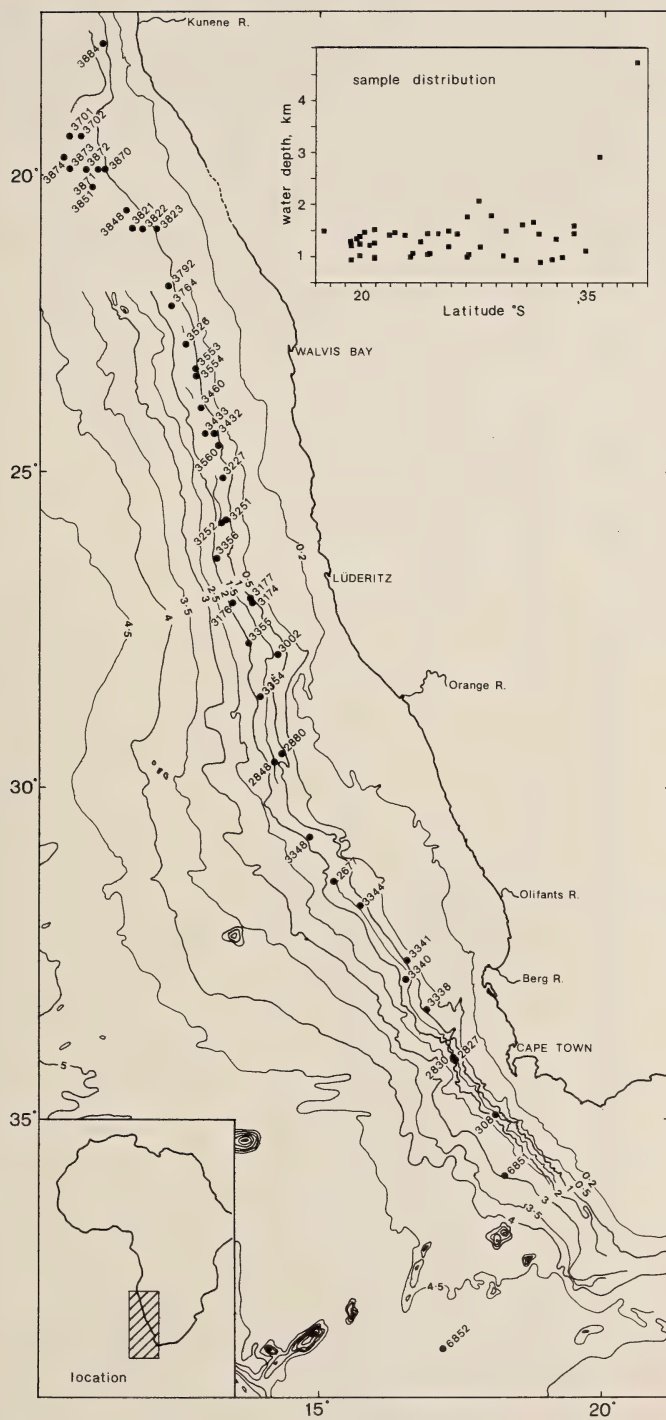
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## INTRODUCTION

Until the advent of the Deep Sea Drilling Project, the main database on deep-sea Ostracoda was the collections and reports from the Challenger expedition (e.g. Brady 1880). Studies of DSDP fossil material (especially Tertiary) have rekindled interest in the subject of bathyal and abyssal ostracod faunas, and a selection of some of the more important publications includes Swain (1970*a*, 1970*b*), Benson (1971, 1972, 1974, 1977, 1978), Peypouquet (1975), Guernet (1982, 1985), Benson & Peypouquet (1983), Whatley (1983, 1985), Whatley *et al.* (1983), Whatley & Coles (1987), Whatley & Ayress (1988), and Hartmann & Hartmann-Schroder (1988). Many of these works relate to specific or fossil taxa, or are regional surveys, with the result that there have been relatively few documentations of Quaternary faunas in relation to oceanographic parameters (e.g. water masses, sea-floor sediments). Important studies that have been made in this category include Rosenfeld & Bein (1978, north-west Africa), Peypouquet & Benson (1980, south-eastern Atlantic), Benson *et al.* (1983, Newfoundland), Cronin (1983, Florida), and Steineck *et al.* (1988, central Pacific).

Our study comprises 46 sample sites in water depths greater than 950 m in the south-eastern Cape Basin, between 17°S and 35°S (Fig. 1). The samples were surface sediments (Quaternary) collected in a Van Veen grab from the University of Cape Town research vessel *Thomas B. Davie* (TBD) and, with the exception of the two deepest sites (TBD 6851, 2 916 m; TBD 6852, 4 736 m), were not stained or preserved in alcohol. A total of 1 059 ostracod valves were recovered, and only one sample was barren (TBD 3226, 970 m). Thirty-seven species were isolated and, of these, six species are allochthonous imports (10 valves, 0.94 per cent total fauna) and four species are residual taxa from upslope lower Neritic assemblages (63 valves). The 27 genuine deep-water taxa are represented by 986 valves. Table 1 lists the locations, water depths, and number of valves for each species. It shows the relatively small numerical database on which we have had to base our study.

Fig. 1. Sample sites in water depths greater than 900 m on the continental margin off south-western Africa. Numbers are University of Cape Town research vessel 'Thomas B. Davie' station numbers for which co-ordinates are given in Table 1. Bathymetry after Dingle *et al.* (1987). Insets show locality, and sample sites on a latitude vs depth scattergram.







<i>Henryhowella melobesoides</i>	<i>Cytheropteron cronini</i>	<i>Cytheropteron</i> sp. 2909	<i>Cytheropteron</i> sp. 2914	<i>Buntonia rosenfeldi</i>	<i>Echinocythereis whatleyi</i>	<i>Ambocythere</i> sp. 3057	<i>Rugocythereis horridus</i>	<i>Dutoitella suhmi</i>	<i>Poseidonamicus major</i>	<i>Trachyleberis</i> sp. 3017	<i>Abyssocythere australis</i>	Indeterminate sp. 62	Indeterminate sp. 23	<i>Buntonia</i> sp. 34	<i>Xestoleberis</i> sp. nov.	<i>Bythocypris</i> sp. 42	Indeterminate fragments	Allocthonous specimens
23		1		2	1												2	2
4				1										1				
31	1			13	2		7								6			
24				2	4									32		4	1	
12													2	2				
1												2						
15	1			8	1		1							1				
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51				1	4								2	9				
4																		
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14				4	3		1											1
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2					4		7	22	105	4	23						4	
										1								

## PHYSIOGRAPHIC AND OCEANOGRAPHIC SETTINGS

The continental margin off south-western Africa forms the eastern edge of the Cape Basin, which is further bounded in a clockwise direction by the Agulhas Ridge, the mid-Atlantic Ridge, and the Walvis Ridge. Abyssal connections to adjacent deep ocean basins ( $>4,5$  km) are probably limited to two small sills: via the central Walvis Ridge to the Angola Basin, and adjacent to the southern tip of Africa to the Agulhas and Mozambique basins. Our samples come from the continental slope and rise off south-western Africa, which has been a sediment-starved margin since mid-Tertiary times (Dingle *et al.* 1987). The principle physiographic features of this region are slumps. These produce minor sea-floor irregularities north of  $34^{\circ}\text{S}$ , and major relief, with numerous small canyons, south of  $34^{\circ}\text{S}$ . Only in the southern region is the continental shelf narrow and shallow enough to have allowed the advance of the coastline (and river discharge) to within 30 km of the shelf break during glacial sea-level lows. Consequently, the potential for allochthonous shelf contaminants on the slope is relatively low over most of the study area, although at  $28^{\circ}\text{S}$  (just south of Lüderitz) the head structures of a large slump lie in a re-entrant of the shelf edge.

The regional physical oceanography along the outer continental margin of south-western Africa has been summarized by Shannon (1985—see pp. 122–125

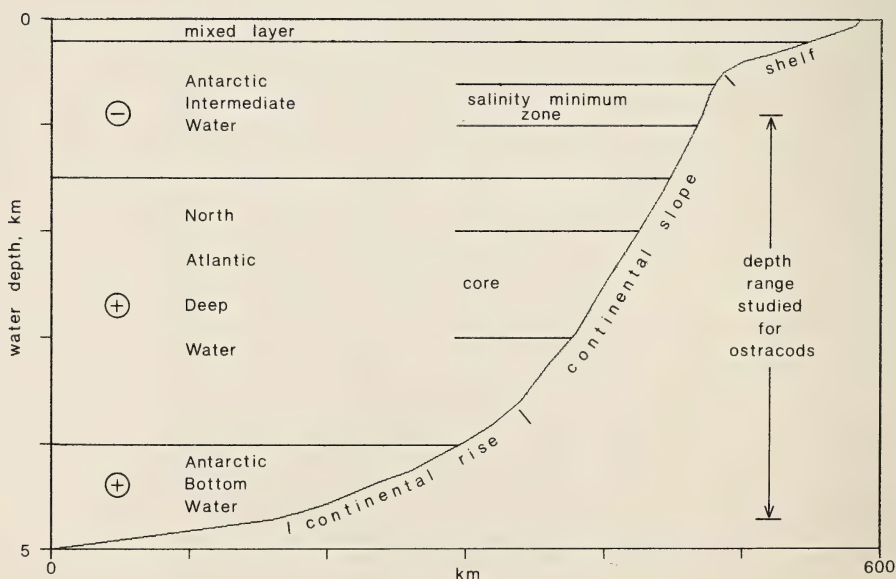


Fig. 2. Schematic water column structure off south-western Africa superimposed on a bathymetric profile across the continental margin south of Lüderitz ( $28^{\circ}\text{S}$ ). Depths for the various water masses are taken from Shannon (1985). Circled symbols indicate direction of water flow: + is towards reader, - is away from reader. Depth range of the ostracod faunas studied is indicated on the right hand side.



for full citation of previous works), who identified three major water masses by their temperature and salinity characteristics. Superimposing these water masses on a bathymetric profile of the south-eastern Atlantic at 28°S (Fig. 2) shows that the outer shelf and upper continental slope (<1,5 km) lie under the northward flowing Antarctic Intermediate Water (AAIW), whereas all the middle to lower slope, and upper continental rise (>1,5 km) lie under the southward flowing North Atlantic Deep Water (NADW). Southward flowing Antarctic Bottom Water (AABW) overlies the lower continental rise and deep ocean floor (>4,0 km), with the consequence that these deeper regions are below the carbonate compensation depth (CCD). The salinity minimum zone within the AAIW lies between 0,6 and 1,0 km on the upper slope, where its base coincides with the bathyal thermocline. As we will discuss later, these two physico-chemical features coincide with the boundary that separates the bathyal from the neritic ostracod faunas.

### TAXONOMY

Abbreviations: ACA = anterior cardinal angle; AM = anterior margin; ATE = anterior terminal element; DM = dorsal margin; LV = left valve; ME = median element; MS = muscle scars; PCA = posterior cardinal angle; PM = posterior margin; PTE = posterior terminal element; RV = right valve; TE = terminal elements; VM = ventral margin.

Figured specimens are stored at the South African Museum under the catalogue numbers SAM-PQ-MF-. SEM numbers refer to unique scanning electron microscope numbers in the collection of RVD.

Subclass OSTRACODA Latreille, 1806

Order PODOCOPIDA Müller, 1894

Suborder PLATYCOPINA Sars, 1866

Family **Cytherellidae** Sars, 1866

Genus *Cytherella* Jones, 1849

The genus *Cytherella* is widely distributed along the continental margin of south-western Africa (Fig. 3). Four species have been recognized and these occupy well-defined depth ranges: *Cytherella dromedaria* Brady, 1880, and *Cytherella* sp. nov. in the Neritic Zone (40–300 m and 115–736 m, respectively), and *C. serratula* (Brady, 1880) and *Cytherella* sp. 3027 in the Bathyal and Abyssal zones (Fig. 4) (1 000–2 070 m, and 2 916 m, respectively). Unlike *Krithe* and *Buntonia*, two important genera that range from shallow- to deep-water environments, neritic species of *Cytherella* do not extend their depth ranges into the Bathyal Zone. In this respect *Cytherella* is similar to *Cytheropteron*.

TABLE 2  
List of genera and species discussed in this paper.

Species	Local depth range (m)	Page
<i>Cytherella</i> Jones, 1849		251
<i>C. serratula</i> (Brady, 1880)	1 000–2 070	
<i>Cytherella</i> sp. 3027	2 916	
<i>Cytheropteron</i> Sars, 1866		258
<i>C. cronini</i> sp. nov.	990–2 070	
<i>Cytheropteron</i> sp. 2909	945	
<i>Cytheropteron</i> sp. 2914	2 070	
<i>Krithe</i> Brady et al., 1874		263
<i>K. capensis</i> sp. nov.	238–1 430	
<i>K. spatularis</i> sp. nov.	392–1 662	
<i>K. rex</i> sp. nov.	2 916	
<i>K. peypouqueti</i> sp. nov.	2 916–4 736	
<i>Krithe</i> sp. 8	530–1 353	
<i>Krithe</i> sp. 9	430–900	
<i>Krithe</i> sp. 4	1 600–2 916	
<i>Krithe</i> sp. 6	1 662–2 916	
<i>Krithe</i> sp. 7	1 600–2 916	
<i>Krithe</i> sp. 19	1 662–2 916	
<i>Krithe</i> sp. 22	2 926	
<i>Parakrithe</i> van den Bold, 1958a		286
<i>Parakrithe</i> sp. 10	945–1 353	
<i>Buntonia</i> Howe, 1935		286
<i>B. rosenfeldi</i> sp. nov.	186–2 070	
<i>Dutoitella</i> Dingle, 1981		293
<i>D. suhmi</i> (Brady, 1880)	2 916	
<i>Abyssocythere</i> Benson, 1971		298
<i>A. australis</i> Benson, 1971	2 916	
<i>Ambocythere</i> van den Bold, 1958b		301
<i>Ambocythere</i> sp. 3057	2 070	
<i>Echinocythereis</i> Puri, 1954		302
<i>E. whatleyi</i> sp. nov.	730–2 916	
<i>Trachyleberis</i> Brady, 1898		309
<i>Trachyleberis</i> sp. 3017	2 916–4 736	
<i>Henryhowella</i> Puri, 1957		310
<i>H. melobesioides</i> (Brady, 1869)	100–2 916	
<i>Rugocythereis</i> gen. nov.		318
<i>R. horridus</i> (Whatley & Coles, 1987)	730–2 916	
<i>Poseidonamicus</i> Benson, 1972		322
<i>P. major</i> Benson, 1972	2 070–2 916	
Indeterminate taxa		328
Indeterminate sp. 62	1 026	
Indeterminate sp. 23	1 060	

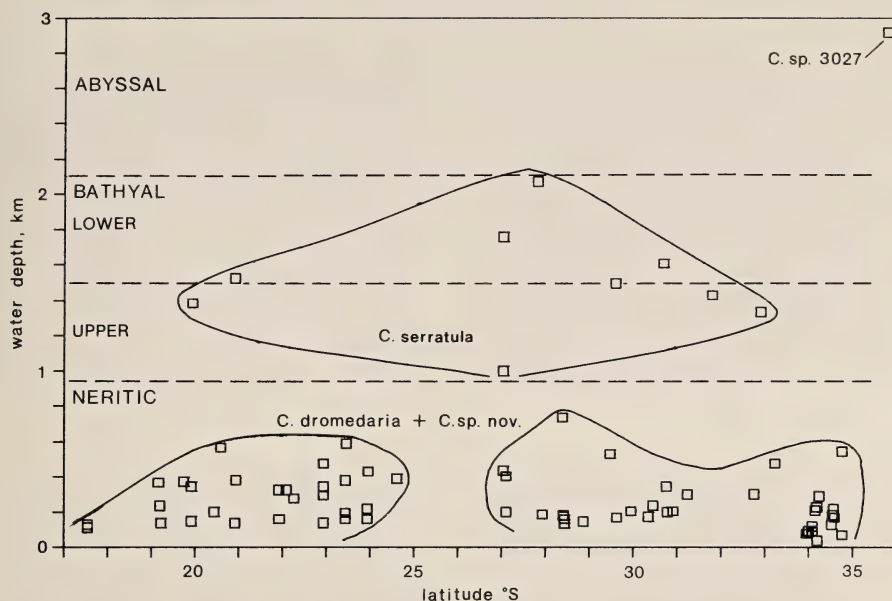


Fig. 3. Latitude and water depth of samples bearing *Cytherella* species. There are two species in each of the Neritic and Bathyal zones: *C. dromedaria* Brady and *Cytherella* sp. nov., and *C. serratula* Brady and *Cytherella* sp. 3027, respectively.

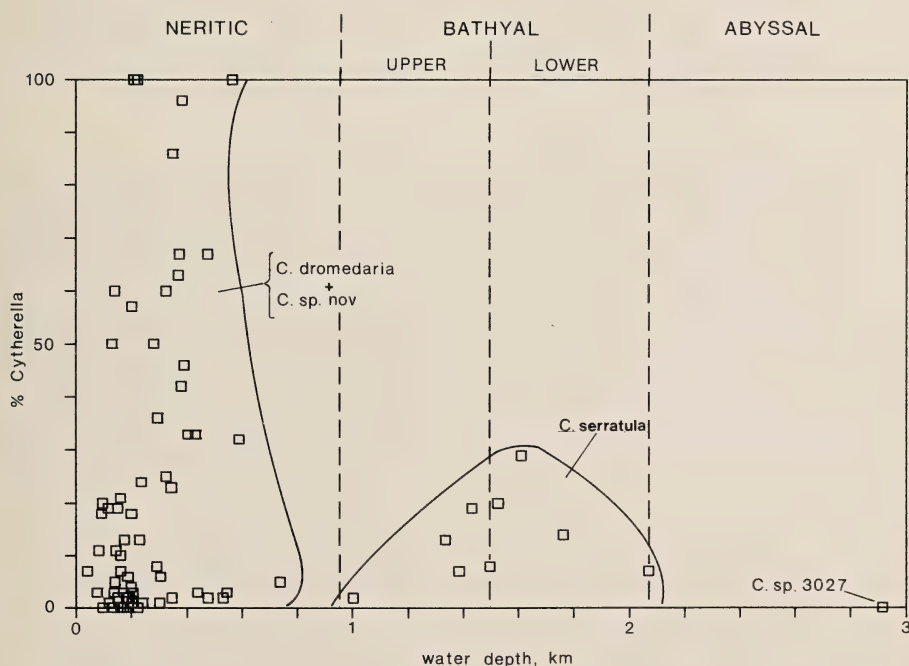


Fig. 4. *Cytherella* species as percentage of total ostracod fauna plotted against water depth. Note concentrations of samples on the continental shelf (<300 m), and at the Upper/Lower Bathyal Zone boundary.



*Cytherella serratula* (Brady, 1880)

## Fig. 5A–C

*Cythere* (?) *serratula* Brady, 1880: 77, pl. 43 (figs 7a–d). Puri & Hulings, 1976: 288–289, pl. 24 (figs 15–16).

*Cytherella serrulata* Brady & Norman, 1896: 713–716, pl. 66 (figs 3–6).

?*Cytherella* sp. 11 Ducasse & Peypouquet, 1979, pl. 1 (figs 3–4).

?*Cytherella* sp. Guernet, 1985: 281, pl. 1 (figs 2, 4).

*Cytherella* sp. B Cronin, 1983, pl. 6 (fig. E).

*Cytherella serratula* (Brady) Whatley & Coles, 1987: 81, pl. 6 (figs 30–31).

*Illustrated specimens*

MF-0422, LV, TBD 3344, 1 430 m.

MF-0423, RV, TBD 3344, 1 430 m.

MF-0424, LV, TBD 3344, 1 430 m.

*Remarks*

Our material shows slight shape and ornamentation differences to the type specimens described by Brady (1880), and the lectotypes illustrated by Puri & Hulings (1976). These, however, are within the range of intraspecific variation found on an inter-ocean basis (R. C. Whatley citing his own data base, pers. comm. 1988). Positive identifications of *C. serratula* (Brady) have been made from the following sites and depths:

Brady (1880) (Recent)—‘Challenger’ site 24, Caribbean, 390 fm (713 m); ‘Challenger’ site 85, Canary Islands, 1 125 fm (2 057 m); ‘Challenger’ site 335, Tristan da Cunha, 1 425 fm (2 605 m).

Brady & Norman (1896) (Recent)—West Africa, 466–1 168 fm (852–2 135 m); Mauretania, 418–675 fm (764–1 234 m); Canary Islands, 487 fm (890 m); Morocco, 600 fm (1 097 m).

Cronin (1983) (Recent)—south-eastern USA continental slope, 462–1 070 m.

Whatley & Coles (1987) (Miocene to Holocene)—DSDP Leg 94 sites, North Atlantic, 2 417–3 022 m.

Present study (Recent)—south-western Africa, 1 000–2 070 m.

These records give a modern depth range of 462–3 022 m in the Atlantic.

*Cytherella* sp. Guernet (1985) from bathyal Eocene sediments at DSDP site 219 on the 90 East Ridge in the Indian Ocean is very similar to *C. serratula* (Brady) in shape and ornamentation, and may be the same species, but differs in having a small, pronounced dorso-median depression. *Cytherella vulgata* Ruggeri, 1962 (as illustrated by Benson 1978, pl. 2 (fig. 3)), from the Upper Pliocene at DSDP site 371 also has a similar shape to *C. serratula*, but has its highest point in the posterior part of the valve and a more extensive covering of small spines and granules in the posterior area. Probably the closest species previously recorded, but not placed in *C. serratula* (Brady), is *Cytherella* sp. 11 of Ducasse & Peypouquet (1979) from bathyal (c. 2 300 m water depth) Pliocene sediments at DSDP site 403 in the Rockall Basin. These specimens differ slightly

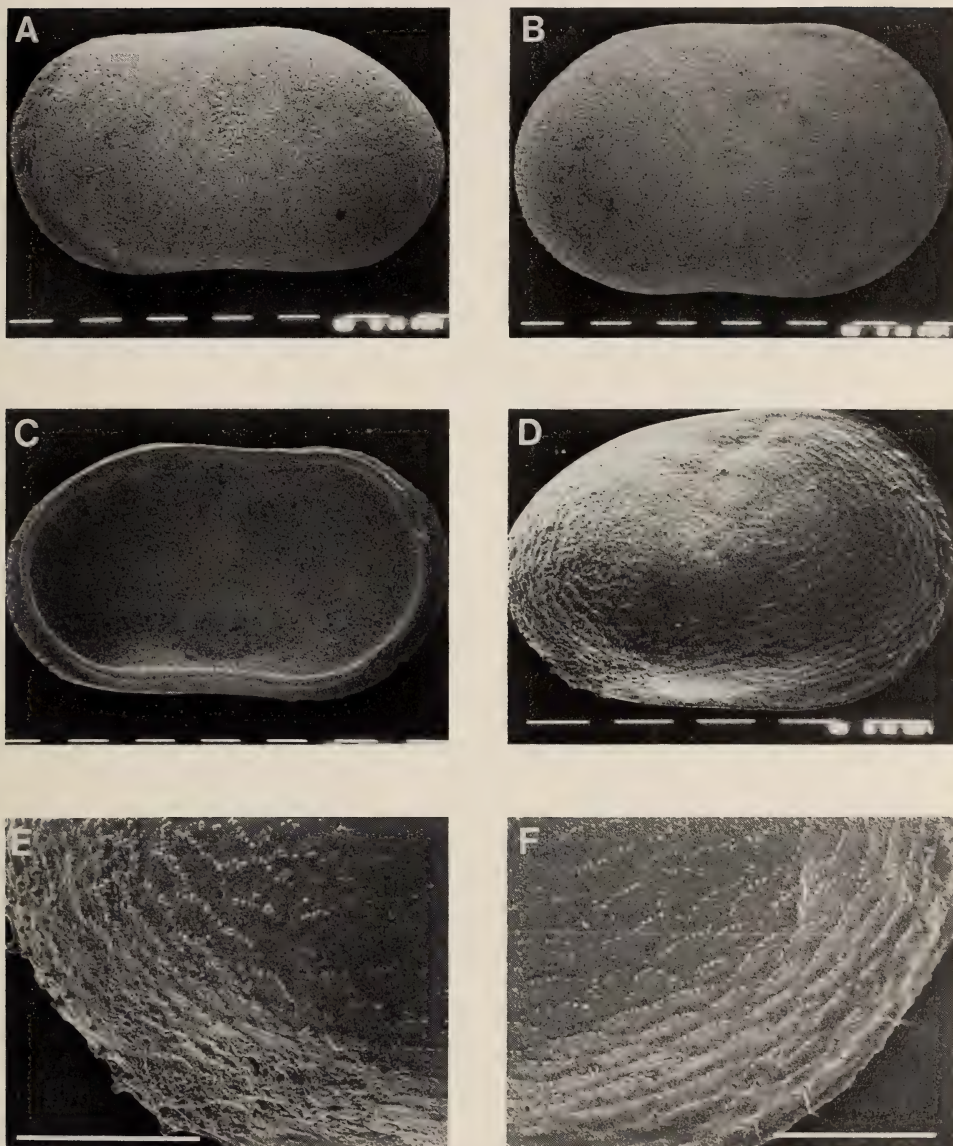


Fig. 5. A-C. *Cytherella serratula* (Brady, 1880), TBD 3344, 1 430 m. A. SAM-PQ-MF-0422, LV, SEM 2584. B. SAM-PQ-MF-0423, RV, SEM 2589. C. SAM-PQ-MF-0424, LV internal view, SEM 2587. D-F. *Cytherella* sp. 3027, SAM-PQ-MF-0425, RV, TBD 6581, 2 916 m. D. External view, SEM 3027. E. Detail, postero-ventral area, SEM 3028. F. Detail, antero-dorsal area, SEM 3029. Scale bar = 100 microns.



from our material in having coarser and more extensive spines in the posterior part of the valve.

Rosenfeld & Bein (1978) recorded smooth species of the genus from the continental slope off north-west Africa, but illustrated only a coarsely pitted species, whereas Peypouquet & Benson (1980) noted the genus at 439–2 154 m in the Cape Basin and 527–2 754 m in the Angola Basin. In neither case did they illustrate or discuss the species present.

Figures 3 and 4 show the geographical and water-depth distributions of *Cytherella serratula* (Brady) in relation to other species of the genus *Cytherella* along the continental margin of south-western Africa. It has been found in sediment samples between approximately 19°S and 33°S (Fig. 3). There is a very well-defined partitioning of the *Cytherella* species with water depth (Fig. 4). In the Neritic Zone, *Cytherella* sp. nov. extends to 736 m and, together with the more restricted *C. dromedaria* Brady, 1880, commonly constitutes greater than 30 per cent of the total ostracod population. There seems to be an hiatus in occurrence of the genus over the depth range 750–1 000 m, coinciding with the Salinity Minimum Zone of the Antarctic Intermediate Water Mass. *Cytherella serratula* appears at the top of the Bathyal Zone, to which it is restricted, and for which its appearance and disappearance constitute one of the defining parameters. In the Bathyal Zone, the genus *Cytherella* (as represented by *C. serratula*) is numerically less important than it is higher up the continental slope, and only reaches 29 per cent in the region of the Upper/Lower Bathyal Zone boundary (1 430–1 610 m). Overall, it forms 3 per cent of the total bathyal ostracod assemblage (fourth most abundant species), but is somewhat more important in the Lower Bathyal Zone, where it averages 9 per cent. Clearly, *Cytherella* is a sensitive indicator of the different water masses, but is less tolerant of the conditions in the colder, more saline Bathyal and Abyssal zones than it is of those in the Neritic Zone. These results are in broad agreement with the data presented by Peypouquet & Benson (1980) from a transect across the continental margin west of Walvis Bay. Plotting their values we obtain Figure 6, which shows a decline in percentage of *Cytherella* in the ostracod populations from greater than 50 per cent in shallow water (<500 m) to less than 10 per cent in the water-depth range 974–1 546 m. In deeper water (2 094 m and 2 117 m) values rise again to approximately 30 per cent.

*Cytherella* sp. 3027

Fig. 5D–F

?*Cytherella* sp. gr. *ovata* (Roemer, 1840) Guernet, 1985: 281, pl. 1 (fig. 1).

*Illustrated specimen*

MF-0425, RV, TBD 6851, 2 916 m.



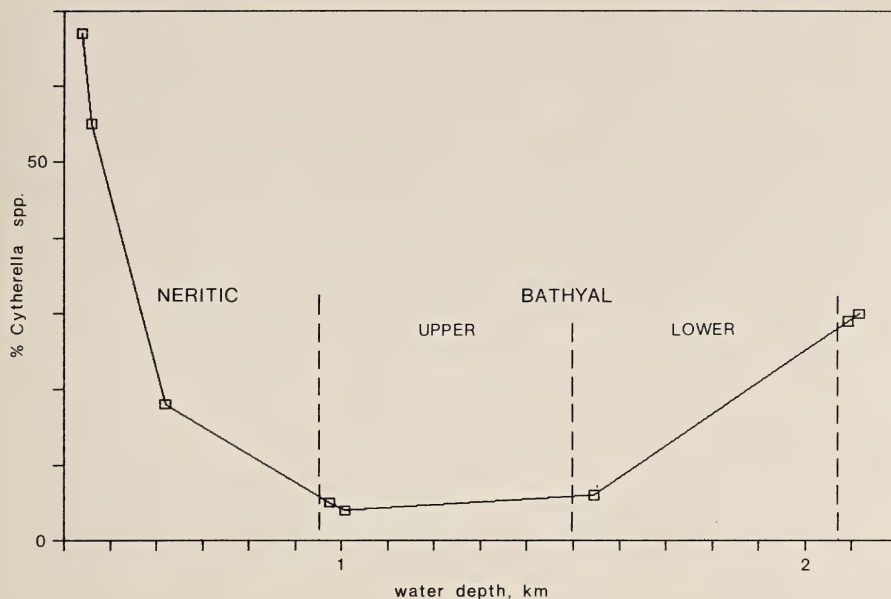


Fig. 6. *Cytherella* species as percentage of total ostracod fauna plotted against water depth for a profile off Walvis Bay. Data computed from Peypouquet & Benson (1980).

#### Remarks

A single RV, possibly a juvenile. It has a distinctive lateral outline, with DM sloping towards the PM, a short straight VM, and broadly rounded AM. The lateral surface has an overall delicate, bead-like reticulation, which is more pronounced in the anterior and posterior areas. There are small spines along the postero-ventral margin, and the AM has a very narrow compressed border with well-separated small pores with setae. There is a triangular depression on the dorso-median surface that extends as a weak sulcus to the valve centre over the MS area.

This is probably a new species, which is confined to the upper part of the Abyssal Zone (2 916 m, TBD 6581).

Guernet (1985) illustrated a very similar specimen from the bathyal Eocene sediments at DSDP site 219 on the 90 East Ridge in the Indian Ocean.

*Cytherella* sp. 3027 is the only representative of the genus *Cytherella* that we encountered in the Abyssal Zone (i.e. >2 070 m, Fig. 4), where it constitutes <0.3 per cent of the total ostracod population. In contrast, Peypouquet & Benson's (1980) samples from similar depths in the northern Cape Basin off Walvis Bay contained approximately 30 per cent *Cytherella*, although they did not illustrate or describe the species involved. This may indicate a shallowing of the CCD in the south-eastern Cape Basin, because below 2 154 m, where they reported very strong dissolution, Peypouquet & Benson (1980, fig. 2) no longer recorded the genus.

Suborder PODOCOPINA Sars, 1866  
 Superfamily Cytheracea Baird, 1850  
 Family **Cytheruridae** Müller, 1894  
 Genus *Cytheropteron* Sars, 1866

On the continental margin off south-western Africa, this genus is represented by 12 species, which occur over a depth range of 40–2 070 m and over a latitudinal range 19°S to 35°S (Figs 7, 8). Nine of these species are confined to the Neritic Zone (where they occur in two distinct groups—inner shelf: 40–90 m, and inner shelf/slope: 80–738 m), and three to the Bathyal Zone. We did not find the genus in the Abyssal Zone (i.e. deeper than 2 070 m).

In the Neritic Zone, *Cytheropteron* is locally relatively abundant (up to 45% total ostracod population in raw data; c. 12% on smoothed curves, Fig. 8), whereas in the Bathyal Zone it does not exceed 6 per cent in any one sediment sample. However, the means of its occurrence in both regions are remarkably constant: 5 per cent in the Neritic Zone, and 4 per cent in the Bathyal Zone. Overall, we found *Cytheropteron* to be numerically more important in the Bathyal Zone: 3,4 per cent of the total ostracod population from samples in which it occurred in the Bathyal Zone, compared to 1,2 per cent from the Neritic Zone. There is, however, a significant difference in the distribution of the various species within the two depth zones. In the Neritic Zone four species

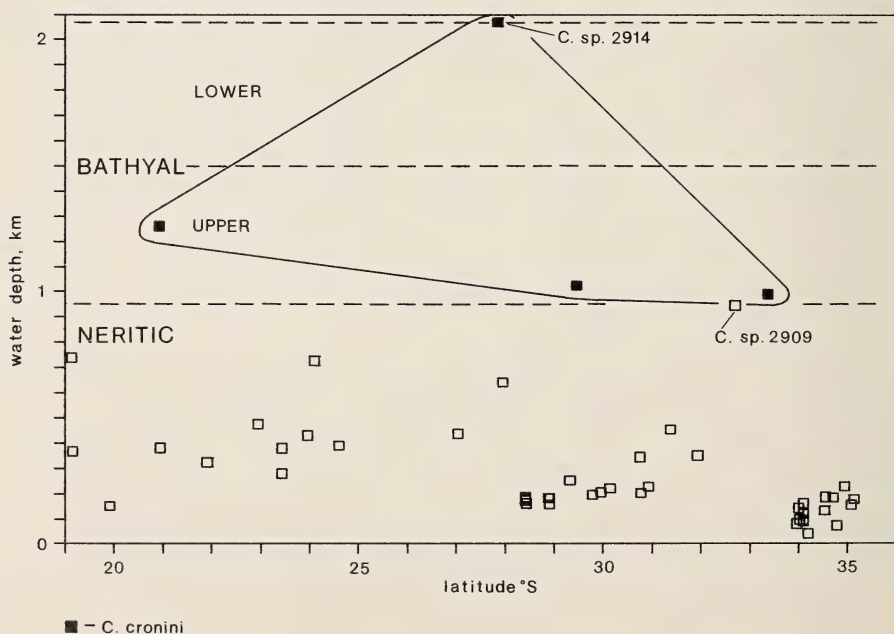


Fig. 7. Latitude and water depth of samples bearing *Cytheropteron* species. There are nine species in the Neritic Zone, and three in the Bathyal Zone (see Fig. 8 for depth ranges).

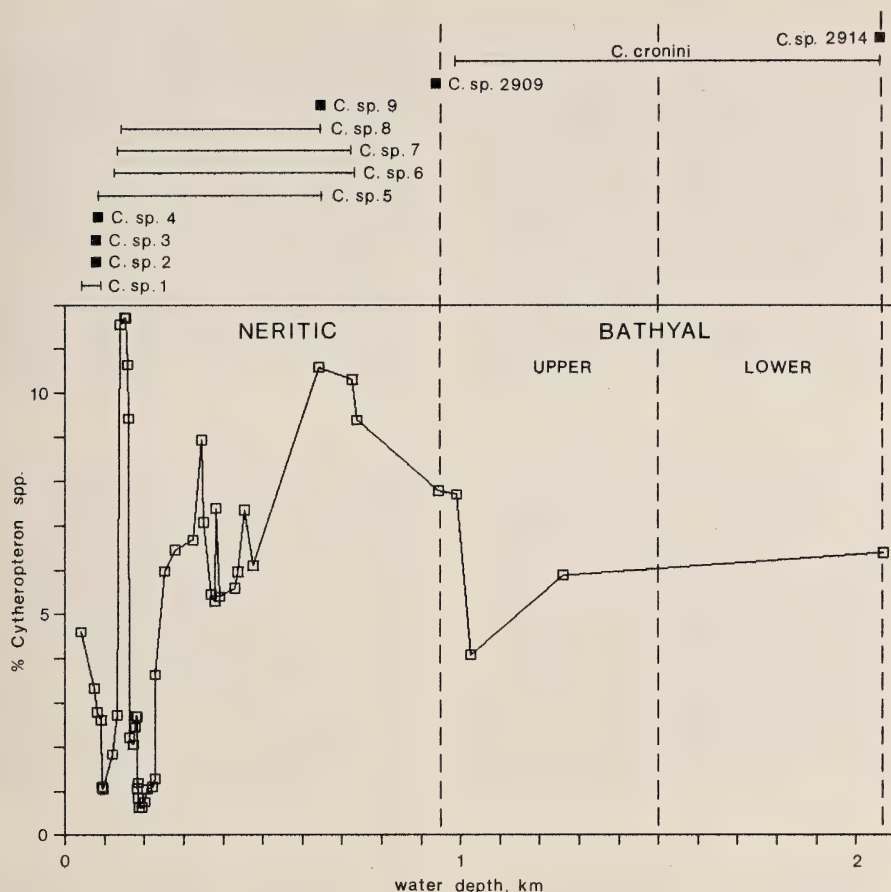


Fig. 8. *Cytheropteron* species as percentage of total ostracod fauna plotted against water depth. Values are five point running means. Depth ranges of species are shown by bars. N.B. Neritic species, *Cytheropteron* species 1-9, are not further discussed herein.

occur with extensively overlapping depth ranges in the outer shelf/upper slope region, whereas in the Bathyal Zone only one species has an extensive depth range (*C. cronini* sp. nov., 990-2 070 m), with the other two species occurring only at the upper and lower limits of the Bathyal Zone (Fig. 8).

The upslope limit of the Bathyal Zone is marked by a decrease in the percentage of the genus relative to the overall ostracod population (mean 12% to 3%) and, with the exception of sample TBD 3355 (2 070 m), all our records for the genus are from the Upper Bathyal Zone (Fig. 7). These data indicate that the genus is sensitive to the physico-chemical changes in the vicinity of the base of the AAIW low salinity layer, and between the AAIW and the NADW masses.



The depth ranges of the three bathyal *Cytheropteron* species from off south-western Africa can be summarized as:

*Cytheropteron* sp. 2909—945 m (uppermost Bathyal Zone)

*Cytheropteron cronini* sp. nov.—990–2 070 m (Bathyal Zone)

*Cytheropteron* sp. 2914—2 070 m (lowermost Bathyal Zone)

Well-documented Quaternary records of the genus from deep-water sites elsewhere are sparse, and confusing. As Whatley & Masson (1979) have observed, there have been few detailed revisions of the nineteenth century works on this genus, with the result that records of earlier-named species are frequently in error.

In their survey in the south-eastern Atlantic, Peypouquet & Benson (1980) recorded the following depth ranges for undefined species of the genus: Angola Basin—527 m; Cape Basin—439–974 m, so that effectively they did not record it from the Bathyal Zone as we have defined it. Off north-west Africa, Rosenfeld & Bein (1978) recorded *Cytheropteron* sp. from 470 m, which was the uppermost part of their 'deep water' Association B fauna. Cronin (1983) listed ten species of *Cytheropteron* from various depths off south-eastern United States, seven of which extend into water depths greater than 1 000 m (his *Cytheropteron* spp. S, D & V, E, B, P, R, and Q). Of these, *Cytheropteron* sp. P is probably conspecific with our new species *C. cronini* from the Cape Basin.

Tressler (1941) illustrated three deep-water species of the genus from the North Atlantic: *Cytheropteron alatum* Sars, 1866 (1 280–4 700 m); *C. hamatum* Sars, 1869 (1 280 m); and *C. inflatum* Brady *et al.*, 1874 (1 955–3 230 m), but comparison of his illustrations with those of Whatley & Masson (1979) indicate that none are conspecific with the original species. Similarly, Benson *et al.*'s (1983) records of *C. alatum* Sars, 1866 (2 560–2 743 m), and *C. testudo* Sars, 1869 (1 380–2 758 m), off Newfoundland are probably mis-identifications. Whatley & Masson (1979) noted that dead specimens of *C. alatum* Sars, 1866, have been found in 830 m in the Rockall Trough (north-eastern Atlantic).

Deep-water species from atypical deep-water settings have been made by Breman (1975a, 1975b), who described *Cytheropteron* sp. and *C. 'adriaticum'* from samples between 144–1 216 m in the Adriatic, and Bonaduce *et al.* (1983), who recorded three species originally described by Bonaduce *et al.* (1976) from 'deep water' sites in the Gulf of Aqaba and the Red Sea: *C. alabarda*, *C. excisum*, and *C. pulcinella*. No water-depth ranges were allocated to individual species.

*Cytheropteron cronini* sp. nov.

Fig. 9A–C

?*Cytheropteron* sp. P Cronin, 1983, pl. 8 (fig. B).

*Derivation of name*

This species is named for Dr T. M. Cronin (US Geological Survey), who first recorded the species or a very close relative of it.

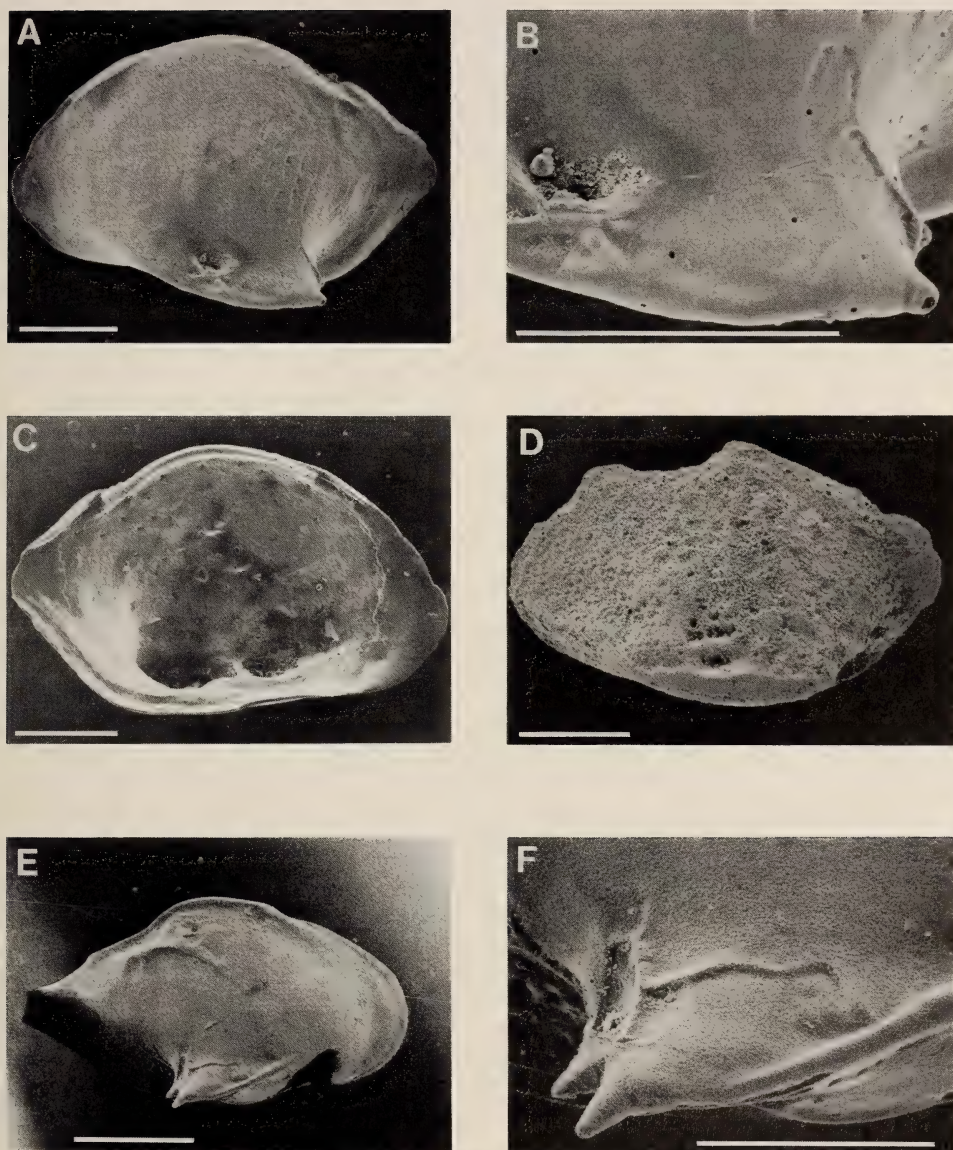


Fig. 9. A-C. *Cytheropteron cronini* sp. nov., SAM-PQ-MF-0426, holotype, LV, TBD 2880, 1 026 m. A. External view, SEM 2911. B. Detail, ala, SEM 2912. C. Internal view, SEM 3093. D. *Cytheropteron* sp. 2909, SAM-PQ-MF-0427, LV, TBD 3341, 945 m, SEM 2909. E-F. *Cytheropteron* sp. 2914, SAM-PQ-MF-0428, RV, TBD 3355, 2 070 m. E. External view, SEM 2914. F. Detail, ala, SEM 2915. Scale bar = 100 microns.



*Holotype*

MF-0426, LV, TBD 2880, 1 026 m.

*Diagnosis*

A dolphin-shaped species with delta-like ala that have a large dimple on their dorsal leading edge. In the dorso-median area there is vertical, slit-shaped reticulation.

*Description*

In lateral outline the AM is asymmetrically rounded, and is inclined ventrally. PM is asymmetric and bluntly caudate, with the apex dorsally directed. DM is strongly arched, VM is asymmetrically convex, sloping ventrally towards the posterior. The central area of the valve is inflated, with a delta-shaped ala that carries a small spine at its apex. There is a large dimple in the anterior proximal area of the ala. Valve surface dorsal to the ala is ornamented with low vertical ribs and slit shaped reticulation. In lateral view there is a small, prominent nick at the posterior end of the DM.

*Dimensions (mm)*

	length	height
MF-0426	0,42	0,28

*Remarks*

This distinctive species (or a close relative) was recorded as *Cytheropteron* sp. P from 347–1 034 m off Florida by Cronin (1983). Species with similar features are: *C. abyssorum* Brady, 1880, from 4 753 m (2 600 fm) off Tasmania, which has a less triangular ala and stronger surface reticulation; *C. trifossata* Whatley & Coles, 1987 (>3 000 m late Quaternary, North Atlantic), which has more prominent ornamentation and a less posteriorly directed ala; and *C. paratissimum* Swain, 1963 (Pleistocene, Arctic Alaska), whose ala are less posteriorly directed and which have 'subvertical furrows' on their lateral surface. *Cytheropteron porterae* Whatley & Coles, 1987 (= *C. alatum* Sars of Benson *et al.* 1983), differs in possessing a thickened leading edge to the ala, and is more coarsely ornamented than *C. cronini* sp. nov. Whatley & Coles (1987) recorded *C. porterae* from the early Pliocene to Quaternary of the North Atlantic.

*Cytheropteron cronini* is the only species of the genus that has wide geographical (21°–33°S) and depth (990–2 070 m) ranges in the Bathyal Zone of the south-eastern Cape Basin (Figs 7, 8).

*Cytheropteron* sp. 2909

Fig. 9D

*Illustrated specimen*

MF-0427, LV, TBD 3341, 945 m.



*Remarks*

One poorly preserved specimen with a distinct bevel along the outer edge of its ala, in the centre of which there is a small depression. The lateral surface may have originally been coarsely punctate. Despite its battered appearance, we conclude that this specimen is not allochthonous because no provenance population has been located farther upslope. It occurs at the top of the Upper Bathyal Zone.

In general shape this species is similar to *Cytheropteron* sp. Q, recorded by Cronin (1983) from 584 m (?382 m) to 1 070 m off the south-eastern United States.

*Cytheropteron* sp. 2914

Fig. 9E-F

*Illustrated specimen*

MF-0428, RV, TBD 3355, 2 070 m.

*Remarks*

A fragile species with a small, sharp ala that bears two small spines, and has a corded leading edge. The sculptured postero-dorsal margin is similar to that of *Cytheropteron* sp. 8 of Ducasse & Peypouquet (1979, pl. 4 (fig. 7)) from the Quaternary of DSDP site 400A (north-eastern Atlantic). The latter has an area of coarse reticulation dorsal to the ala, which in *Cytheropteron* sp. 2914 is covered by a feint, longitudinally sinuous ridge. This species is a close relative of *C. syntomoalatum* Whatley & Coles, 1987 (see pl. 2 (fig. 27)), from the late Pliocene to Quaternary of the North Atlantic, particularly in possessing a mid-dorsal 'cross'. Differences in ornamentation and structure of the ala apex may indicate that the two are not conspecific.

*Cytheropteron* sp. 2914 was encountered only in the lowermost part of the Lower Bathyal Zone.

Family *Cytherideidae* Sars, 1925Genus *Krithe* Brady, Crosskey & Robertson, 1874

The genus *Krithe* and the closely related genus *Parakrithe* have conventionally been regarded as indicators of 'deep' water (e.g. Van Morkhoven 1962), and use has recently been made of variations in shell architecture to semi-quantitatively predict palaeo-water depths and dissolved oxygen levels (e.g. Peypouquet 1975, 1979; Donze *et al.* 1982). The latter studies have been based on numerous morphotypes that, whilst they have not attempted to systematically isolate species, have shown that this group is taxonomically complex and diverse (e.g. Peypouquet 1979). Whatley (1983) recorded that, with the exception of

*Cytheropteron* (57 species), *Kriithe* (54 species) is the most diverse genus in the Quaternary ostracod faunas of the bathyal and abyssal regions of the south-western Pacific.

Similarly, *Kriithe* (together with one species of *Parakriithe*) and *Cytheropteron* are the two most diverse genera in the deep-water faunas off south-western Africa (12 species each), whereas in the Abyssal Zone the genus *Kriithe* is the most abundant taxon. It occurs across the entire latitudinal range of our study area (17°S to 38°S), and is found over a more extensive water-depth range than any other genus (238–4 736 m, Fig. 10). With one exception (*Kriithe* sp. 9), all the species are found in either bathyal or abyssal depths, and five also occur in the Neritic Zone (Fig. 13). On a regional scale, variations in the abundance of *Kriithe* within the overall ostracod populations have been used (together with *Henryhowella melobesioides* (Brady, 1869) and *Buntonia rosenfeldi* sp. nov.) to help identify the limits of the faunal zones off south-western Africa (see Figs 54, 55).

Figure 11 shows that the abundance of *Kriithe* species (as a percentage of the total ostracod fauna) varies greatly over the water-depth range of the genus, and that there is not a simple progressive increase in values oceanward. This can be further emphasized when mean values for individual depth zones are examined: Figure 12 shows that, although the overall trend is Neritic (19%) through

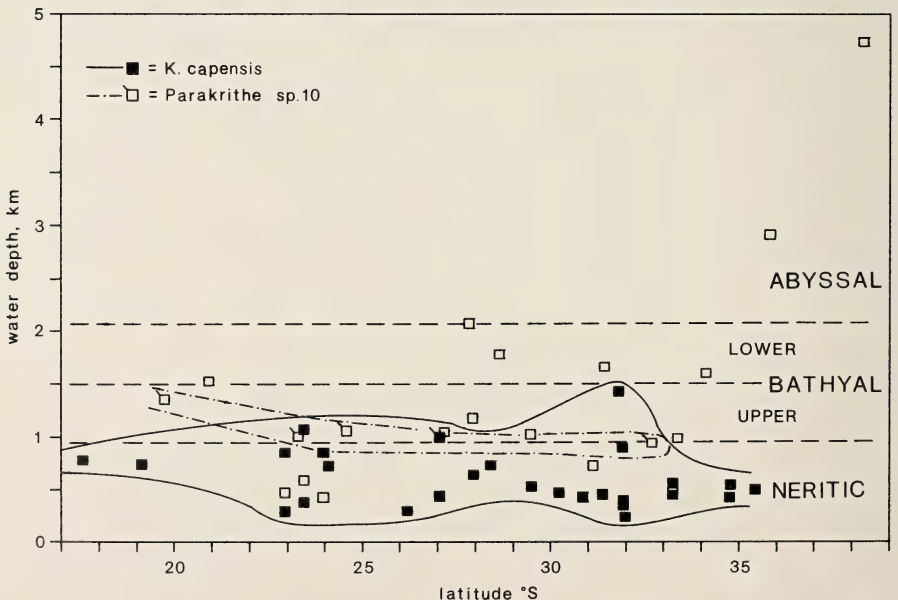
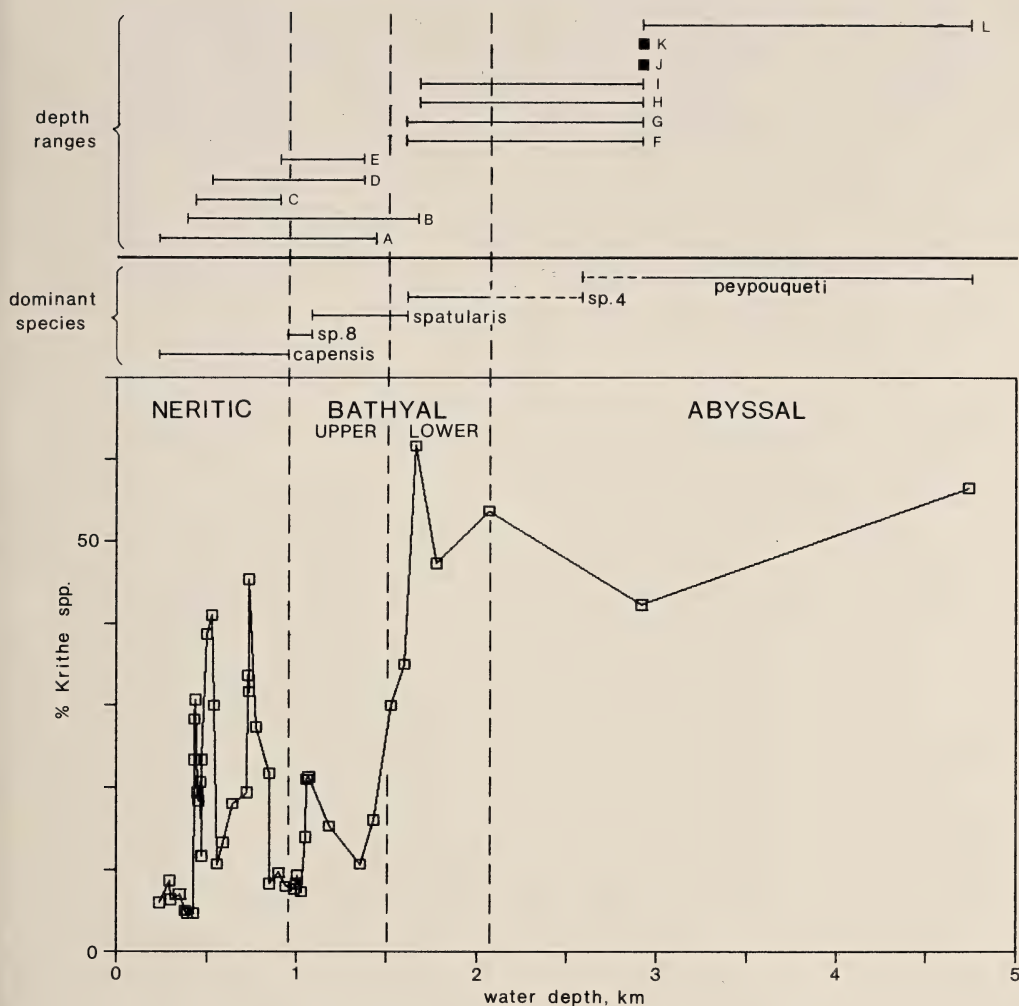


Fig. 10. Latitude and water depth of samples bearing *Kriithe* species and *Parakriithe* sp. 10. The distributions of *Kriithe capensis* sp. nov. and *Parakriithe* sp. 10 are outlined.



- |                             |                          |
|-----------------------------|--------------------------|
| A. <i>K. capensis</i>       | G. <i>K. sp. 7</i>       |
| B. <i>K. spatularis</i>     | H. <i>K. sp. 6</i>       |
| C. <i>K. sp. 9</i>          | I. <i>K. sp. 19</i>      |
| D. <i>K. sp. 8</i>          | J. <i>K. rex</i>         |
| E. <i>Parakrithe sp. 10</i> | K. <i>K. sp. 22</i>      |
| F. <i>K. sp. 4</i>          | L. <i>K. peypouqueti</i> |

Fig. 11. *Krithe* species (including *Parakrithe sp. 10*) as percentage of total ostracod fauna plotted against water depth. Values are three point running means. In the upper part of the diagram 'depth ranges' show bars for total range of individual species of *Krithe* and one species of *Parakrithe* identified A-L in the list in lower part of figure. *Krithe sp. 9*, which is a neritic taxon, is included for completeness. 'Dominant species' shows depth range bars for particular species dominating the *Krithe* assemblage, and are derived from variations in abundance shown in Figure 13.



Bathyal (24%) to Abyssal (42%), there is a decrease from Neritic into Upper Bathyal (13%), and a decrease from Lower Bathyal (51%) into Abyssal. These fluctuations can be related to the environmental tolerances of particular species, and we recognize two groups: an Upper *Krithe* Fauna that occurs in the Neritic and Upper Bathyal zones (238–1 500 m); and a Lower *Krithe* Fauna that occurs in the Lower Bathyal and Abyssal zones (1 500–4 736 m) (Figs 11, 13A–B, 14).

Throughout most of the Neritic Zone, the Upper *Krithe* Fauna is dominated by *Krithe capensis* sp. nov., but this species declines sharply in abundance across the Neritic/Bathyal boundary, below which it is effectively replaced by *Krithe* sp. 8. *Krithe capensis* also suffers a temporary decline in abundance between approximately 500 m and 700 m water depth, where there is also a sharp decline in the importance of the genus as a whole across the upper boundary of the salinity minimum zone of the AAIW. Within this narrow depth range, as well as over the lower part of the Upper Bathyal Zone (where the genus as a whole is again relatively poorly represented), *Krithe spatularis* sp. nov. replaces *K. capensis* as the dominant species.

The genus *Krithe* reaches a low level of abundance within the ostracod populations at the base of the Upper Bathyal Zone (i.e. at the base of the AAIW mass) where, over the depth range 1 430 m to 1 525 m, all four extant

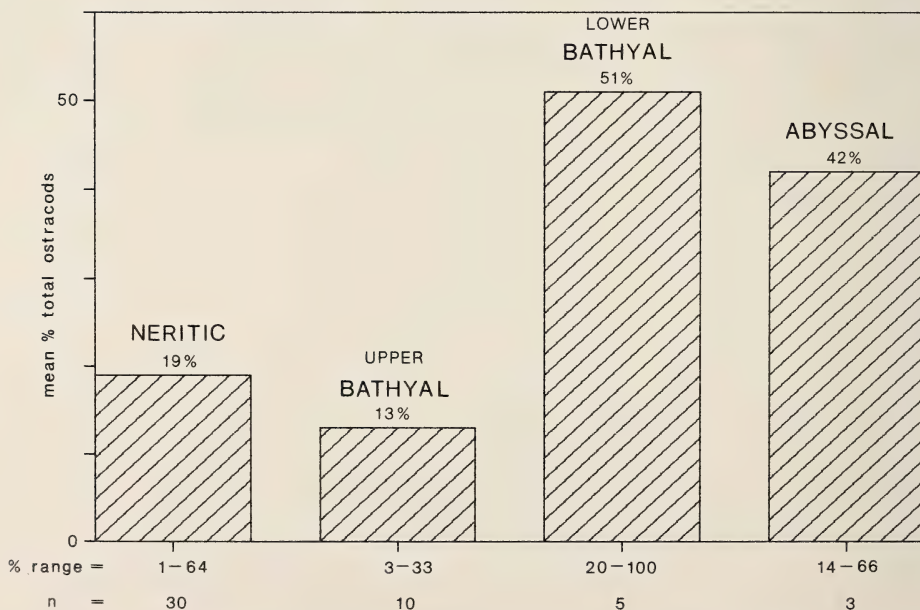


Fig. 12. The mean percentage of *Krithe* species for the four depth zones. Values are calculated on samples in which *Krithe* occurs, and not on the overall ostracod fauna. Mean value for the Bathyal Zone is 24%; n = number of samples.

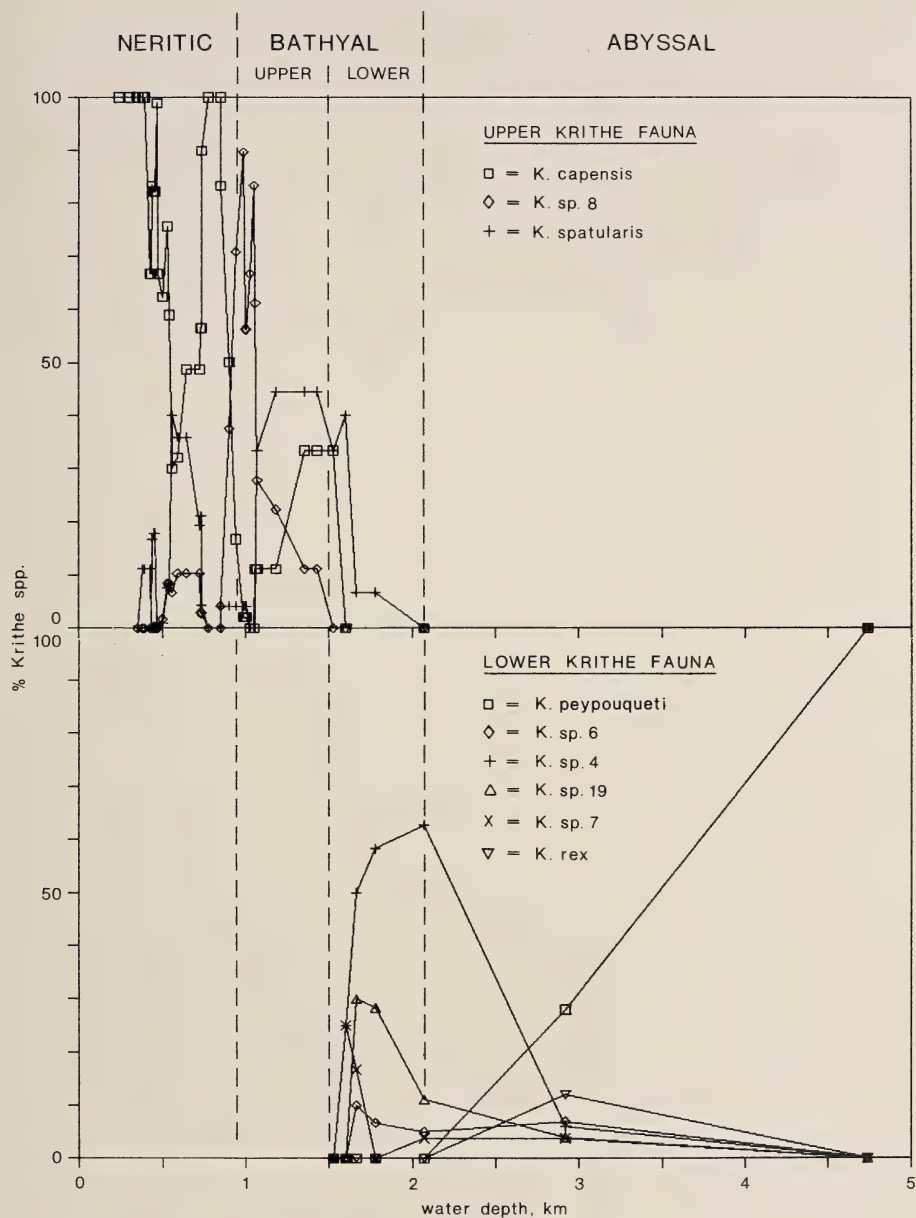


Fig. 13. Variation in abundance of individual *Krithe* species with water depth (plotted as a percentage of the *Krithe* assemblage). A. Upper *Krithe* Fauna (three-point means). B. Lower *Krithe* Fauna (three-point means, and raw data in deepest sample). Ranges over which particular species dominate are shown in Figure 11.

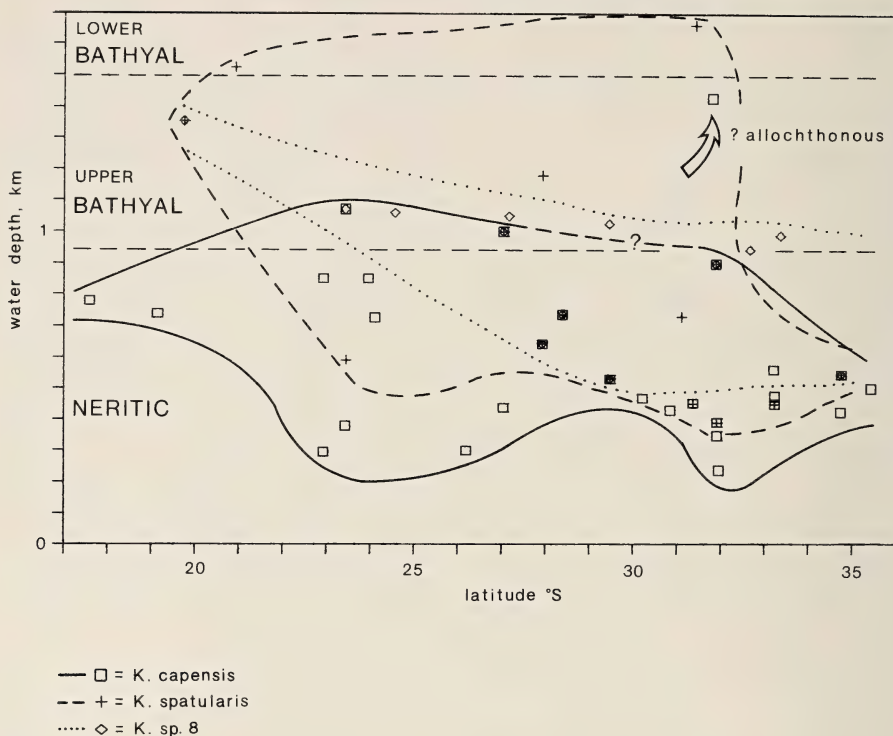


Fig. 14. Latitude and water depth of samples bearing *Krithe capensis*, *K. spatularis*, and *Krithe* sp. 8. The open arrow locates a possible allochthonous occurrence of *K. capensis*.

species of the Upper *Krithe* Fauna die out (*K. capensis*, *K. spatularis*, *Krithe* sp. 8, and *Krithe* sp. 9). There is a dramatic increase in the abundance of the genus in the Lower Bathyal Zone with the incoming of four species of the Lower *Krithe* Fauna (*Krithe* sp. 4, *Krithe* sp. 6, *Krithe* sp. 19, and *Krithe* sp. 7). Of these, *Krithe* sp. 4 dominates the Lower Bathyal and upper parts of the Abyssal zones, before it and the three other species are themselves replaced by the true abyssal species at 2 916 m. The most important abyssal taxon is the relatively small, globular *Krithe peypouqueti* sp. nov.

A summary of the species of *Krithe* that dominate at the various depths off south-western Africa is given in Figure 11.

Peypouquet & Benson (1980) recorded the distribution of *Krithe* and *Parakrithe* in their transect west of Walvis Bay, but the relative sparsity of data points precludes a detailed comparison with our data (Fig. 15). The overall picture is of a significant increase in abundance across the Neritic/Bathyal boundary, and a decrease in Abyssal depths. The highest values occur within the Bathyal Zone, and in this respect their data agrees with our own.



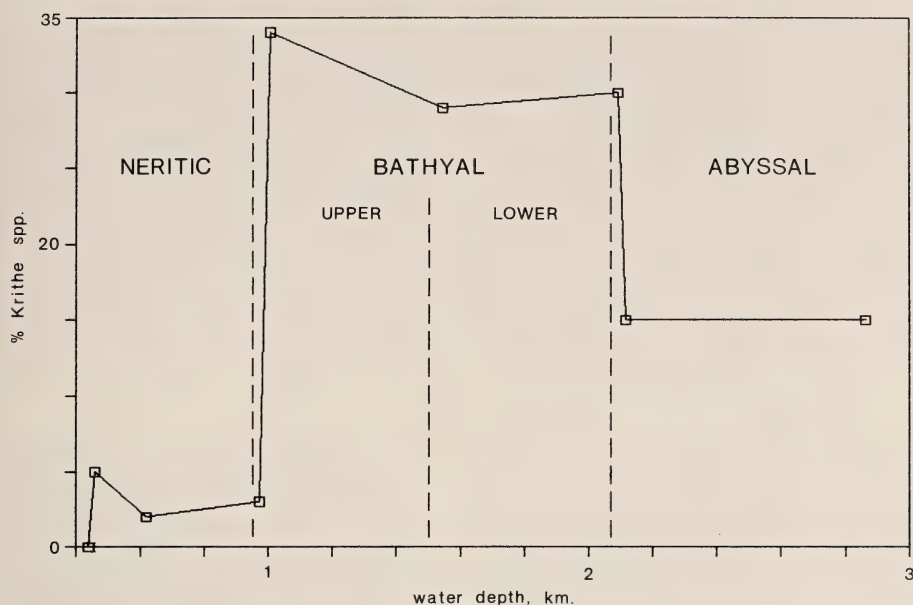


Fig. 15. *Krithe* species as percentage of total ostracod fauna plotted against water depth for a profile off Walvis Bay. Data computed from Peypouquet & Benson (1980).

*Krithe capensis* sp. nov.

Figs 16A–C, 17A, 18D

*Krithe* spp. Boomer, 1985: 57–58, pl. 4 (fig. 63).

*Derivation of name*

From the Cape Basin.

*Holotype*

MF-0429, LV, TBD 2879, 530 m.

*Paratypes*

MF-0431, LV, TBD 2879, 530 m.

MF-0430, RV, TBD 3577, 453 m.

MF-0450, LV, TBD 3577, 453 m.

*Diagnosis*

In lateral view, the highest point of the valve lies in the posterior third, over a broadly rounded postero-dorsal arch. VM is straight, AM is broadly rounded.

### Description

In external view, the valves have a high, broadly rounded arch over the posterior dorsal region. AM in the LV is broadly rounded and almost symmetrical, whereas the AM in the RV is slightly upturned and there is a subtle antero-dorsal step. The PM depression is prominent and elliptical, but partly hidden in internal lateral view. The anterior vestibule is moderately large and has two lobes on the dorsal side. The anterior inner margin descends from the dorsal margin in almost a straight line, and forms an acute angle antero-ventrally. MS have a partly subdivided dorsal-most adductor, and a lobed anterior scar.

### Dimensions (mm)

	length	height
MF-0429	0,91	0,50
MF-0431	0,90	0,51
MF-0430	0,95	0,50
MF-0450	0,99	0,50

The mean length/height ratio of the type specimens is 1,86, which distinguishes *Krithe capensis* in the local deep-water faunas from all but *Krithe* sp. 4 (Figs 19, 20).

### Remarks

We have difficulty in assigning *K. capensis* sp. nov. to the 'ecotypes' described by Peypouquet (1979), but on balance it has most in common with his category C.

*Krithe capensis* is quite close to *K. nibelaensis* Dingle from the Campanian to Eocene of southern Africa (Dingle 1981; Frewin 1987), but their MS patterns differ in the shape of the anterior scar, and the former species has a more arched postero-dorsal valve outline. Rosenfeld & Bein (1978, pl. 1 (fig. 20)) illustrated a species with a similar inner margin outline to *K. capensis*, which they allocated to *K. producta*? Brady, 1880. Our species differs from theirs in its more arched postero-dorsal outline and less prominent and incised posterior depression. The lectotype of *K. producta* Brady, 1880 (Puri & Hulings 1976), has a more rounded PM and broadly arched DM outline than *K. capensis*. Benson & Peypouquet (1983, pl. 5 (fig. 5)) illustrated a specimen (*Krithe* sp. C23) from the Lower Miocene of DSDP site 516 that has a similar shaped vestibule to *K. capensis*, but this species has parallel VM and DM.

Off south-western Africa, we have found *Krithe capensis* within the latitudinal range 17°S to 35°S (Fig. 10). Its depth range is 238–1 430 m (a total of 1 192 m), which includes the outer shelf (Neritic Zone) through to the uppermost part of the Lower Bathyal Zone. This suggests that *K. capensis* is the most euryhaline and eurythermal *Krithe* species in our study area (34,9–34,6‰ to <34,4‰, 10°C to 3,2–3,6°C). Variations in its abundance in relation to other species of the genus (Fig. 13) indicate that *K. capensis* is the dominant species

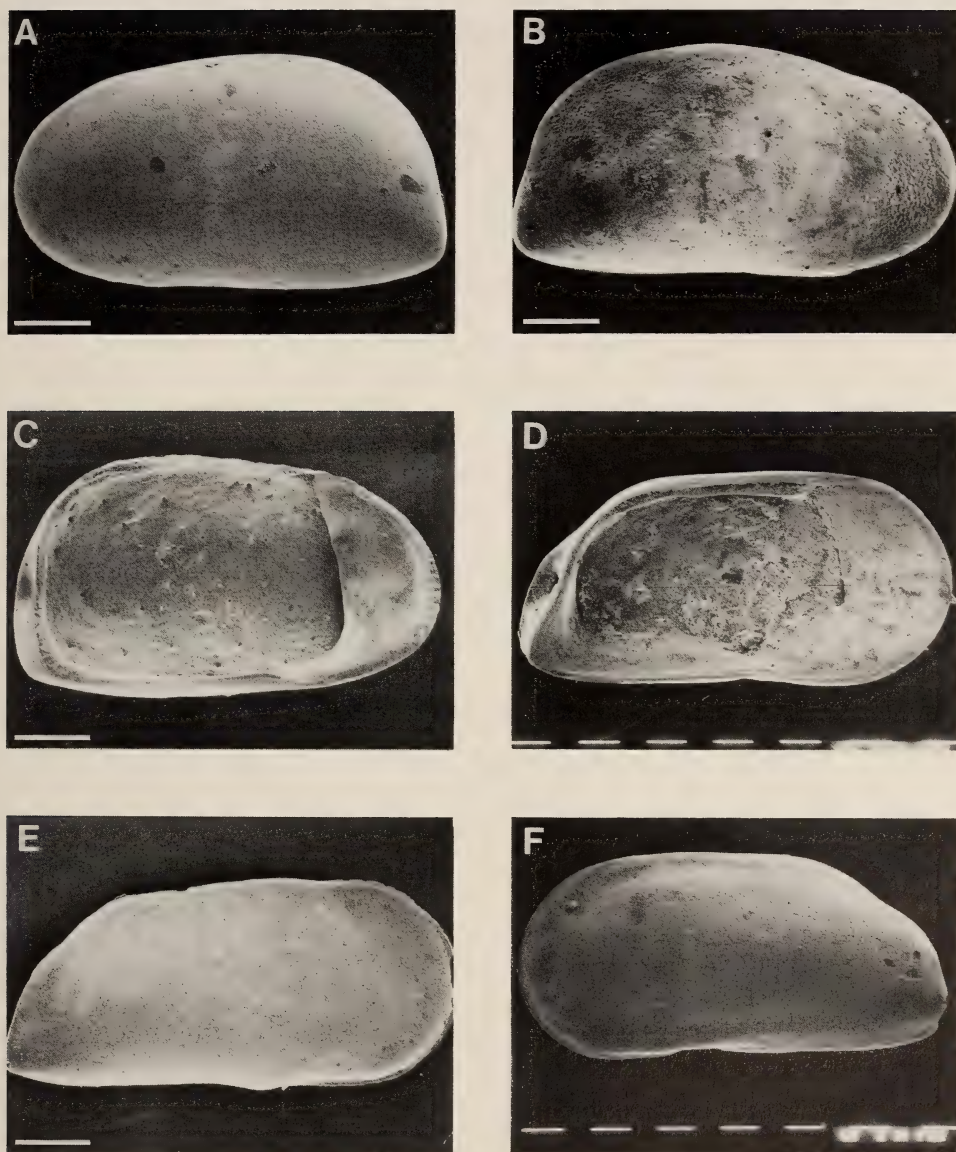


Fig. 16. A-C. *Krithe capensis* sp. nov. A. SAM-PQ-MF-0429, holotype, LV, TBD 2879, 530 m, SEM 2709. B. SAM-PQ-MF-0430, RV, TBD 3577, 453 m, SEM 2714. C. SAM-PQ-MF-0431, LV internal view, TBD 2879, 530 m, SEM 2710. D-F. *Krithe spatularis* sp. nov. D. SAM-PQ-MF-0432, holotype, LV internal view, TBD 2978, 736 m, SEM 2707. E. SAM-PQ-MF-0433, RV, TBD 2978, 736 m, SEM 2705. F. SAM-PQ-MF-0434, LV, TBD 3177, 1 000 m, SEM 2702. Scale bars = 100 microns.



on the continental shelf and uppermost slope, but over the depth range c. 500–700 m it is replaced by *K. spatularis* sp. nov. This coincides with the part of the AAIW mass that lies immediately above the Salinity Minimum Zone (see Fig. 2). Within the Salinity Minimum Zone, *K. capensis* reverts to its dominant position but, from about 950 m to the depth at which it dies out (1 430 m), it declines rapidly in abundance. At the Neritic/Bathyal boundary (950 m) it is replaced by *Krithe* sp. 8., and at deeper levels by *K. spatularis* sp. nov. Its lower limit is apparently defined by the AAIW/NADW shear zone boundary (Upper/Lower Bathyal boundary). All our evidence suggests that in the south-eastern Cape Basin, *K. capensis* is the most tolerant of low-salinity conditions of all the species of the genus.

A more critical assessment of the geographical distribution of *Krithe capensis* (Fig. 14) suggests that the deepest site at which the species has been located may in fact represent an allochthonous occurrence. We suspect this because the three sites astride the Neritic/Bathyal boundary lie along a wide front from which station TBD 3344 (1 430 m) is isolated. If this is the case, then the depth range of this species is 238–1 071 m (a total of 833 m), and *K. capensis* would more correctly be considered a neritic species that only straggles into the deep-water assemblages in the Upper Bathyal Zone, just below the base of the Salinity Minimum Zone of the AAIW. At present we have insufficient data to confirm this suspicion, and take the data at face value.

*Krithe spatularis* sp. nov.

Figs 16D–F, 17B, 18E

*Derivation of name*

Latin *spatula*—spoon, allusion to spoon- or spatula-like lateral outline.

*Holotype*

MF-0432, LV, TBD 2978, 736 m.

*Paratypes*

MF-0433, RV, TBD 2978, 736 m.

MF-0434, LV, TBD 3177, 1 000 m.

MF-0451, RV, TBD 3555, 590 m.

*Diagnosis*

Species with a compressed, spatula-shaped anterior lateral outline, and a deep, cleft-like posterior depression.

*Description*

In external lateral view, AM is broadly and symmetrically rounded. The antero-dorsal and AM areas are compressed, giving a spatula-like appearance.

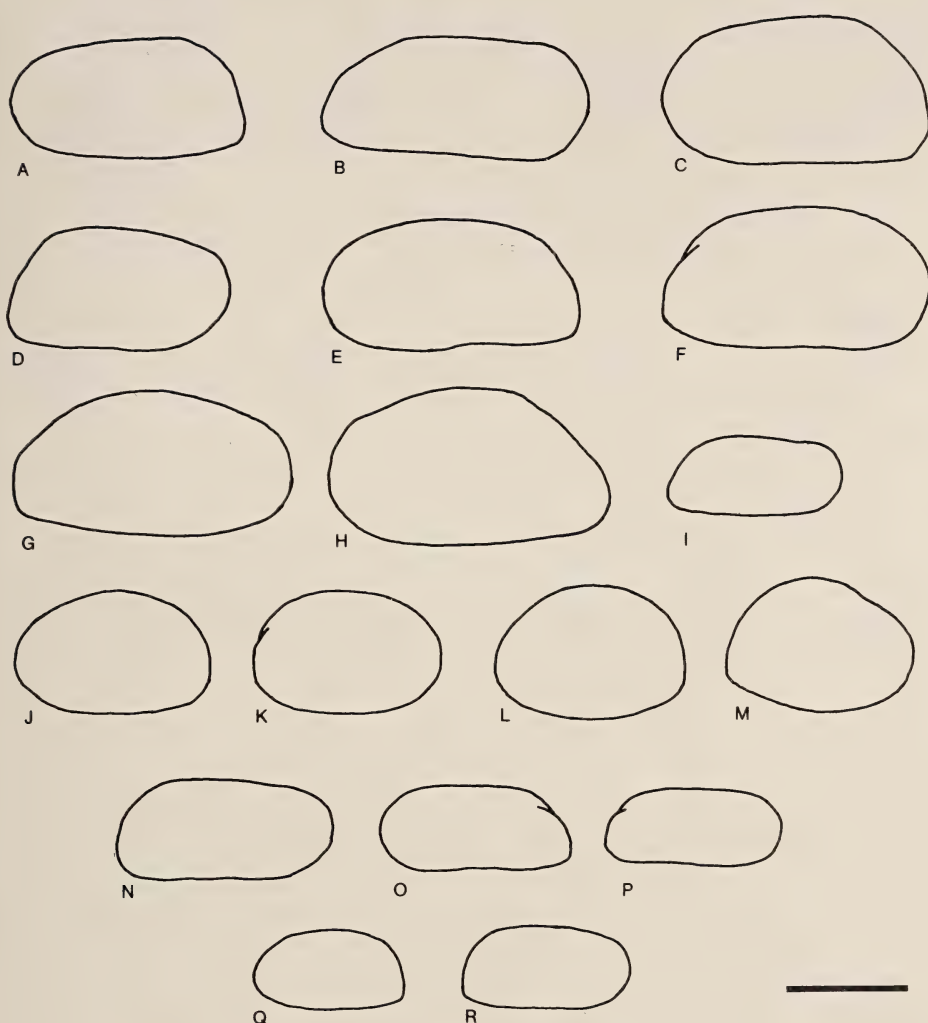


Fig. 17. Outlines of various species of *Krithe* and *Parakrithe*. A. *Krithe capensis* sp. nov., SAM-PQ-MF-0450, LV, TBD 3577, 453 m. B. *Krithe spatularis* sp. nov., SAM-PQ-MF-0451, RV, TBD 3555, 590 m. C. *Krithe* sp. 8, SAM-PQ-MF-0452, LV, TBD 3177, 1 000 m. D. *Krithe* sp. 4, SAM-PQ-MF-0453, RV, TBD 3355, 2 070 m. E-F. *Krithe* sp. 7, TBD 6851, 2 916 m. E. SAM-PQ-0454, LV. F. SAM-PQ-MF-0446, RV. G-H. *Krithe rex* sp. nov., TBD 6851, 2 916 m. G. SAM-PQ-MF-0456, RV. H. SAM-PQ-MF-0438, LV. I. *Parakrithe* sp. 10, SAM-PQ-MF-0449, RV, TBD 3553, 1 003 m. J-K. *Krithe* sp. 6, TBD 6851, 2 916 m. J. SAM-PQ-MF-0457, LV. K. SAM-PQ-MF-0445, RV. L-M. *Krithe peypouqueti* sp. nov., TBD 6851, 2 916 m. L. SAM-PQ-MF-0441, LV. M. SAM-PQ-MF-0439, RV. N. *Krithe* sp. 9, SAM-PQ-MF-0443, RV, TBD 3524, 475 m. O-P. *Krithe* sp. 19, TBD 6851, 2 916 m. O. SAM-PQ-MF-0447. Q-R. *Krithe* sp. 22, TBD 6851, 2 916 m. Q. SAM-PQ-MF-0458, LV. R. SAM-PQ-MF-0448, RV.

Scale bar = 500 microns.

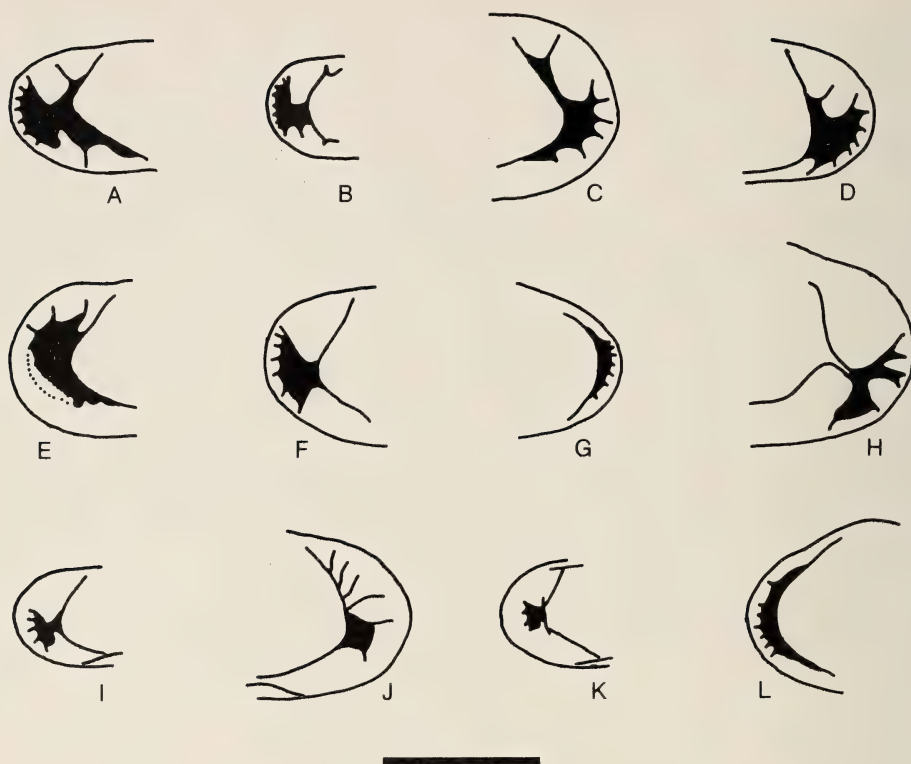


Fig. 18. Details of anterior marginal areas of *Krithe* and *Parakrithe*, placed in order of lower depth limit of species. All internal views. A. *Krithe* sp. 9, SAM-PQ-MF-0443, RV, TBD 3524, 475 m. B. *Parakrithe* sp. 10, SAM-PQ-MF-0449, RV, TBD 3553, 1 003 m. C. *Krithe* sp. 8, SAM-PQ-MF-0452, LV, TBD 3177, 1 000 m. D. *Krithe capensis* sp. nov., SAM-PQ-MF-0450, LV, TBD 3577, 453 m. E. *Krithe spatularis* sp. nov., SAM-PQ-MF-0451, RV, TBD 3555, 590 m. F. *Krithe* sp. 4, SAM-PQ-MF-0453, RV, TBD 3355, 2 070 m. G. *Krithe* sp. 6, SAM-PQ-MF-0457, LV, TBD 6851, 2 916 m. H. *Krithe rex* sp. nov., SAM-PQ-MF-0438, ?female, LV, TBD 6851, 2 916 m. I. *Krithe* sp. 19, SAM-PQ-MF-0447, RV, TBD 6851, 2 916 m. J. *Krithe* sp. 7, SAM-PQ-MF-0454, LV, TBD 6851, 2 916 m. K. *Krithe* sp. 22, SAM-PQ-MF-0448, RV, TBD 6851, 2 916 m. L. *Krithe peypouquetii* sp. nov., SAM-PQ-MF-0439, holotype, RV, TBD 6851, 2 916 m. Scale bar = 500 microns.

DM and VM parallel, although there is a slight concavity at about mid-length in the VM. PM asymmetric, sloping steeply to a ventral apex. In internal view, the posterior depression is very prominent and lies in a deep, ventrally open cleft. Anterior vestibule is large and posteriorly wide. Outline of inner margin is symmetrically rounded, with an anterior apex.



*Dimensions (mm)*

	length	height
MF-0432	1,09	0,55
MF-0433	1,02	0,50
MF-0434	1,11	0,55
MF-0451	1,10	0,49

The mean length/height ratio of the type specimens is 2,07, which is the highest value we have recorded amongst the large species of *Krithe* in our study (Figs 19, 20).

*Remarks*

The distinctive shape of the new species has no close analogues from southern Africa, but is similar to the following species from elsewhere: *K. hiwanneensis* Howe & Lea, 1936, from the Oligocene of Louisiana (which is not compressed anteriorly); *K. oertlii* Dieci & Russo, 1967, from the Miocene of Italy (which does not have a straight DM); and *K. vandenboldi* Steineck, 1981, from the Miocene of Jamaica (which is a smaller species with a slightly concave VM outline, and a differently shaped anterior vestibule).

*Krithe spatularis* sp. nov. would seem to fit into the 'ecotype' *Krithe* sp. F of Peypouquet (1979), which he suggested is an indicator of low dissolved O<sub>2</sub> in the water column.

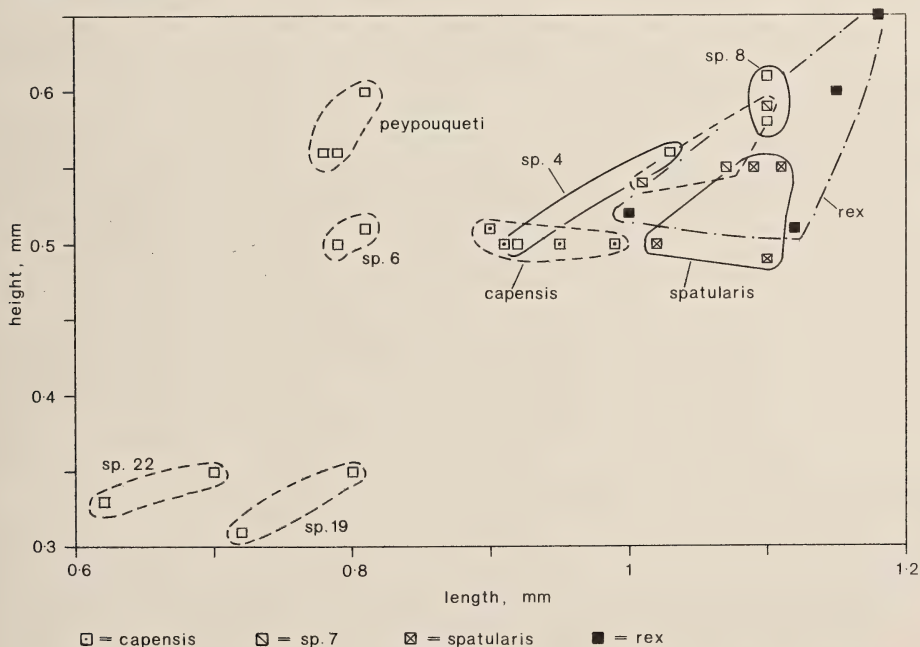


Fig. 19. Length versus height scattergram of *Krithe* species. Data points are specimens illustrated herein.

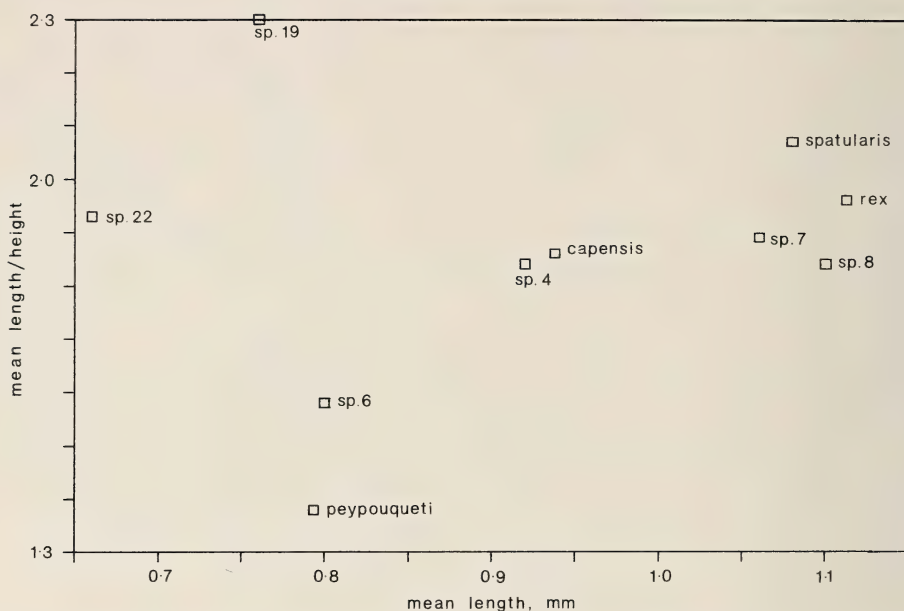


Fig. 20. Ratios of mean length/mean height plotted against mean lengths for the illustrated specimens of the various species of *Krithe*.

Off south-western Africa, *K. spatularis* has a latitudinal range 19°S to 35°S, and a depth range 392–1 662 m (a total of 1 272 m) (Figs 13, 14). It is most abundant (relative to other species of the genus) at those levels where *K. capensis* is relatively unsuccessful, i.e. immediately above the Salinity Minimum Zone in the AAIW (lower Neritic Zone), and in the lower part of the Upper Bathyal Zone, although we never recorded it exceeding 3 per cent of the total ostracod population. Despite a greater depth range than *K. capensis*, *K. spatularis* probably tolerates a narrower salinity and temperature range (34.8–34.5‰ to <34.6‰; 8.5–6°C to 3.2–2.8°C), because of its deeper upper depth limit.

***Krithe rex* sp. nov.**

Figs 17G–H, 18H, 21A–D

?*Krithe* sp. C Cronin, 1983, pl. 10 (figs B–C).

*Derivation of name*

Latin *rex*—king, allusion to large, bold species.

*Holotype*

MF-0435, RV, male, TBD 6851, 2 916 m.

*Paratypes*

MF-0436, RV, female, TBD 6851, 2 916 m.

MF-0437, RV, male, TBD 6851, 2 916 m.

MF-0438, LV, ?female, TBD 6851, 2 916 m.

MF-0456, RV, male, TBD 6851, 2 916 m.

*Diagnosis*

Large species with humped DM and convex VM. There is a prominent antero-dorsal step in lateral outline.

*Description*

A large species, with a distinctive, bold shape and marked sexual dimorphism. In external lateral view, AM is broadly rounded, PM is truncated and short, sloping to a postero-ventral apex. The DM is strongly arched, particularly in the shorter (presumed) females, in which the convex VM is also more prominently developed. The central area of the valves is somewhat inflated. In internal view, the posterior depression is clearly visible but is neither large nor incised. The anterior inner lamella is wide but the vestibule is relatively small and complex in shape, lying between the anterior margin and two large lobe-like re-entrants in the line of concrescence. The inner margin outline has a small neck-like incision that links the vestibule to the interior of the shell. This may represent a weak zone that preferentially suffers abrasion. The MS consist of a forward pointing V-shaped anterior scar, with a small super-adjacent scar, and four elongate adductors, the most dorsal of which is partially subdivided.

*Dimensions (mm)*

	length	height
MF-0435	1,15	0,60
MF-0436	1,18	0,73
MF-0437	1,12	0,51
MF-0438	1,18	0,65
MF-0456	1,17	0,60

The mean length/height ratio of the type specimens is 1,96. When plotted against valve length (Fig. 20), *Krithe rex* is seen to be a more elongate taxon than *Krithe* sp. 7 and *Krithe* sp. 8, with which it has an overlapping length/height field on the scattergram (Fig. 19).

*Remarks*

This is the largest species of the genus *Krithe* in the ostracod populations off south-western Africa (the holotype is 1 150 microns in length), and can be assigned to Peypouquet's (1979) category D2.

No species analogous to *Krithe rex* has been recorded from southern Africa, but the following species from elsewhere are similar in general appearance: *Krithe cubensis* van den Bold, 1946, from the Oligocene of Cuba (which is less inflated, and possesses relatively large vestibules); *Krithe morkhoveni* van den



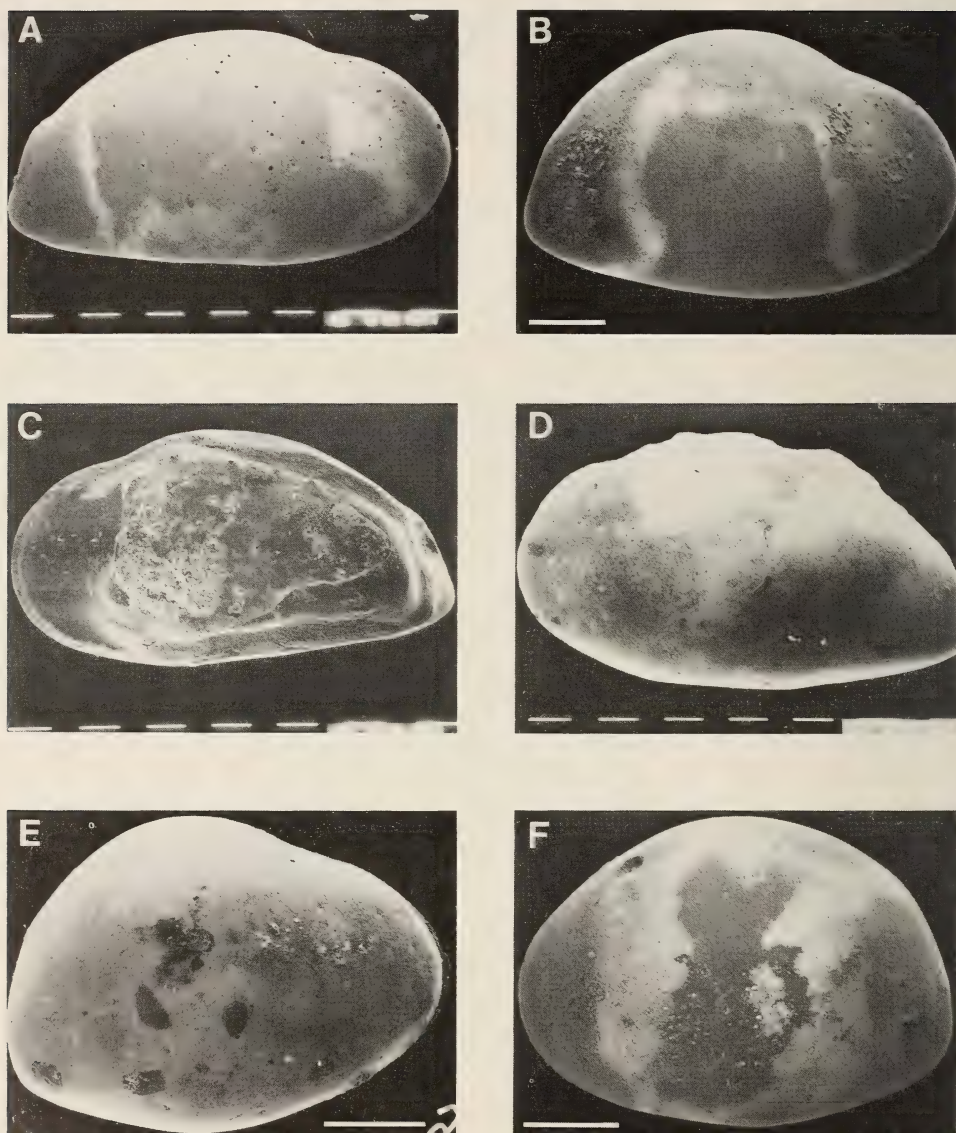


Fig. 21. A-D. *Krithe rex* sp. nov. TBD 6851, 2 916 m. A. SAM-PQ-MF-0435, holotype, male, RV, SEM 2691. B. SAM-PQ-MF-0436, female, RV, SEM 2694. C. SAM-PQ-MF-0437, male, RV internal view, SEM 2701. D. SAM-PQ-MF-0438, ?female, LV, SEM 2695. E-F. *Krithe peypouqueti* sp. nov. TBD 6851, 2 916 m. E. SAM-PQ-MF-0439, holotype, RV, SEM 2695. F. SAM-PQ-MF-0440, LV, SEM 2695.

Scale bars: B = 200 microns, others = 100 microns.

Bold, 1960, from the Miocene of Trinidad (which is a much smaller species, has a different MS pattern, and possesses relatively large vestibules); *K. trinidadensis* van den Bold, 1958a, from the Oligocene to Miocene of Trinidad (which has a less strongly arched DM and the males have a more acuminate PM outline than *K. rex* sp. nov.). Brady (1880, pl. 27 (fig. h)) illustrated a species as *Krithe producta* (probably not conspecific with the lectotype designated by Puri & Hulings 1976), which lacks the LV antero-dorsal step.

Cronin (1983) illustrated a species (*Krithe* sp. C, pl. 10 (figs B-C)) from his deepest sample off Florida (1 070 m), which may be conspecific with *Krithe rex* sp. nov. and is the closest relative that we have observed in the literature. Guérinet's *Krithe* sp. 1 (1985, pl. 1 (fig. 16)) from the Upper Eocene of DSDP site 214 (90 East Ridge, Indian Ocean) also has a similar lateral outline, although its VM is somewhat less convex.

Off south-western Africa, we have recovered *Krithe rex* at only one site (TBD 6851) at a water depth of 2 916 m, where it constitutes 3 per cent of the total ostracod population and 6 per cent of the *Krithe* population. In our area it is clearly an abyssal species, but if Cronin's (1983) *Krithe* sp. C is conspecific, then in the north-western Atlantic at least, the species ranges into the depths equivalent to the Upper Bathyal Zone as we define it in the south-eastern Atlantic.

*Krithe peypouqueti* sp. nov.

Figs 17L-M, 18L, 21E-F, 22A

*Derivation of name*

The species is named for Dr J.-P. Peypouquet (University of Bordeaux) for his work on the genus *Krithe*.

*Holotype*

MF-0439, RV, TBD 6851, 2 916 m.

*Paratypes*

MF-0440, LV, TBD 6851, 2 916 m.

MF-0441, LV, TBD 6851, 2 916 m.

*Diagnosis*

A globular species with a rounded DM, and a strong antero-dorsal step in the RV lateral outline.

*Description*

A squat, globular species in lateral view. AM broadly rounded, PM asymmetrically rounded, truncated in LV. DM strongly arched and rounded, with a prominent antero-dorsal step in the RV. VM broadly convex. Central valve area is inflated. In internal view, the inner margin runs approximately parallel to the AM, and the inner lamella and vestibule are narrow.



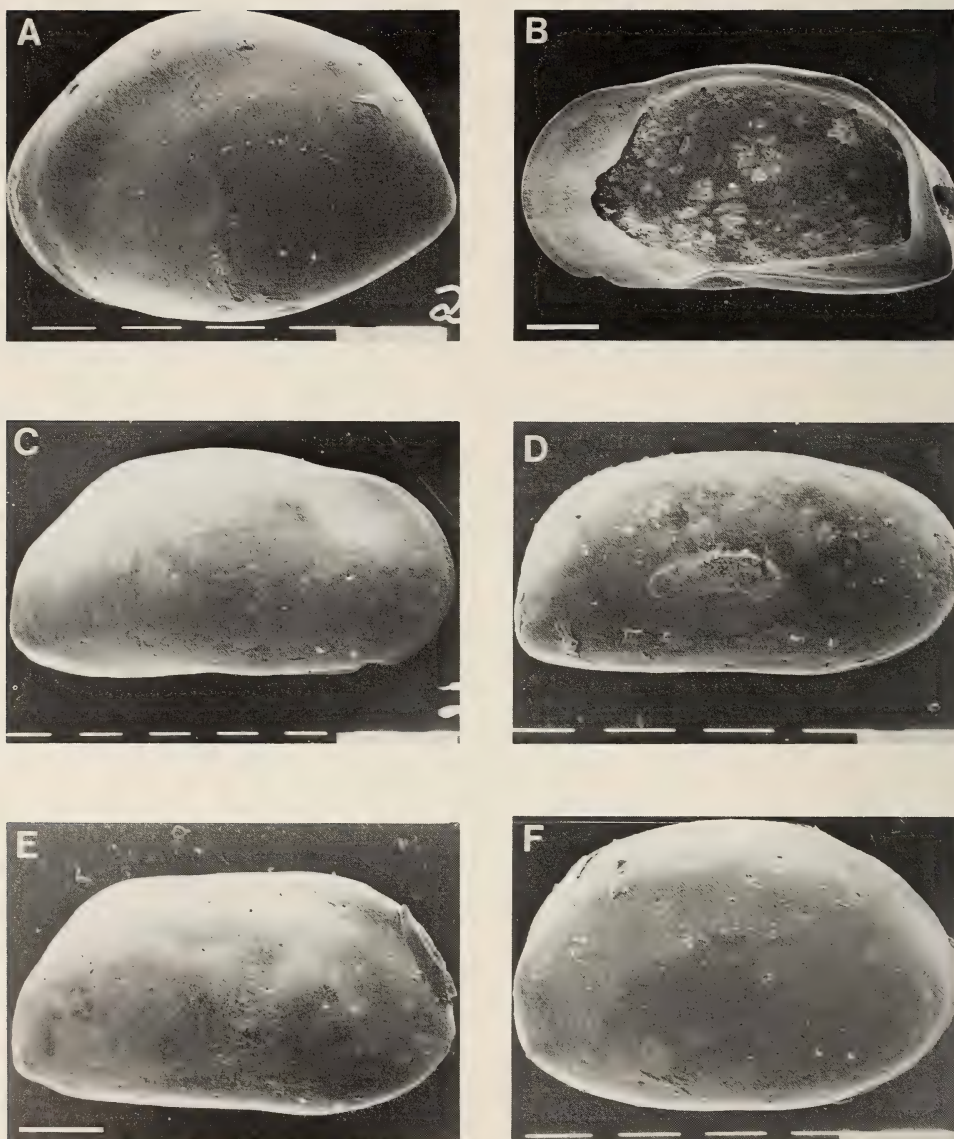


Fig. 22. A. *Krithe peypouqueti* sp. nov., SAM-PQ-MF-0441, LV, TBD 6851, 2 916 m. B-C. *Krithe* sp. 8, SAM-PQ-MF-0442, TBD 3177, 1 000 m. B. RV internal view, SEM 2715. C. External view. D. *Krithe* sp. 22, SAM-PQ-MF-0448, RV, TBD 6851, 2 916 m. E. *Krithe* sp. 4, SAM-PQ-MF-0444, RV, TBD 3355, 2 070 m. F. *Krithe* sp. 6, SAM-PQ-MF-0445, RV, TBD 6851, 2 916 m. Scale bars = 100 microns.



*Dimensions (mm)*

	length	height
MF-0440	0,81	0,60
MF-0439	0,78	0,56
MF-0441	0,79	0,56

The mean length/height ratio of the type specimens is 1,38, which combined with its mean length values (0,79 mm) easily distinguishes *Krithe peypouqueti* from all other species of the genus that occur off south-western Africa (Figs 19, 20).

*Remarks*

The species most similar in lateral outline to *Krithe peypouqueti* sp. nov. that we have encountered in the literature is a specimen recorded by Guernet (1983, pl. 1 (fig. 15)) under *Krithe* sp. 1 (his category is clearly poly-specific) from the Upper Eocene of DSDP site 214 on the 90 East Ridge. However, this species has a wide inner lamella.

Off south-western Africa, *Krithe peypouqueti* has a depth range 2 916–4 736 m, and is one of the most abundant ostracod species in the Abyssal Zone. At Site TBD 6851 (2 916 m), it constitutes 13 per cent of the total ostracod fauna (second in abundance to *Poseidonamicus major*) and 28 per cent of the *Krithe* population (the most abundant species of the genus). At site 6852 (4 736 m, where only three valves were recovered), *Krithe peypouqueti* forms 66 per cent of the total ostracod fauna.

OTHER SPECIES OF *KRITHE**Neritic/Bathyal species*

*Krithe* sp. 8  
Figs 17C, 18C, 22B–C

*Illustrated material*

MF-0442, RV, TBD 3177, 1 000 m.  
MF-0452, LV, TBD 3177, 1 000 m.

*Remarks*

This is a relatively large species (see Fig. 19) that has a distinctive postero-dorsal arch, giving it a 'humped back' appearance in lateral view. Its overall outline is similar to *Krithe rex* sp. nov., but it is somewhat less elongate (mean length/height ratio = 1,84) (Fig. 20). The posterior depression is deep, rounded, and set in a wide flat furrow. The inner lamella is relatively wide, with large anterior vestibules, and the outline of the inner margin is asymmetrically

rounded, with an antero-ventral apex. MS consist of an irregular U-shaped and small elongate anterior set, and four elongate adductors, the dorsalmost of which is almost subdivided.

*Krithe* sp. 8 has a depth range of 530–1 353 m off south-western Africa (i.e. Neritic to Upper Bathyal) and, although it is generally rare (1–6% total ostracod fauna), the species appears to opportunistically exploit an environmental niche at the Neritic/Bathyal boundary. Here, straddling the base of the Salinity Minimum Zone, it is the most abundant species in the *Krithe* population (up to 11% of the total ostracod fauna, and >80% of the *Krithe* fauna), locally supplanting the two important taxa in the Upper *Krithe* Fauna (*Krithe capensis* and *K. spatularis*) (see Figs 11, 13).

*Krithe* sp. 9

Figs 17N, 18A, 23C

*Illustrated material*

MF-0443, RV, TBD 3524, 475 m.

*Remarks*

Although not a bathyal species, we include a record of *Krithe* sp. 9 for completeness. This is a sub-quadrate, elongate species with a large and complex anterior vestibule. It has a depth range of 430–900 m, so that its lower range overlaps with *Krithe capensis*, *K. spatularis*, and *Krithe* sp. 8.

*Bathyal/Abyssal species*

Four species of *Krithe* appear immediately below the Upper/Lower Bathyal boundary (i.e. at the top of the NADW mass). These constitute the taxa in the upper part of the Lower *Krithe* Fauna: *Krithe* sp. 4, *Krithe* sp. 6, *Krithe* sp. 7, and *Krithe* sp. 19 (Figs 11, 13).

*Krithe* sp. 4

Figs 17D, 18F, 22E

*Illustrated material*

MF-0444, RV, TBD 3355, 2 070 m.

MF-0453, RV, TBD 3355, 2 070 m.

*Remarks*

This is a relatively large quadrate species, with a distinctively truncated PM outline in lateral view. On the length/height scattergrams, this species occupies a field between the species with mean lengths >1,00 mm and *K. capensis* (Figs 19, 20). The anterior vestibule is moderately large and widens anteriorly from a

narrow posterior 'neck'. The outline of the inner margin has a rounded apex at about mid-height. None of our adult specimens had well-preserved hinges but there appears to be a strong, elongate, tooth-like structure at the anterior end of the RV ME. The single anterior MS has three anteriorly directed lobes.

*Krithe* sp. 4 has a depth range 1 600–2 916 m off south-western Africa. It is the dominant species of the Lower *Krithe* Fauna in the Lower Bathyal and upper Abyssal levels (2% of total ostracod fauna), below which it is replaced by *K. peypouqueti* (Figs 11, 13). This distribution pattern suggests that *Krithe* sp. 4 is tolerant only of the physico-chemical environments found in the upper part of the NADW mass.

*Krithe* sp. 6

Figs 17J–K, 18G, 22F

*Illustrated material*

MF-0445, RV, TBD 6851, 2 916 m.

MF-0457, LV, TBD 6851, 2 916 m.

*Remarks*

A moderate-sized species with a semi-elliptical outline in lateral view, in which the RV posterior margin has a small re-entrant in the vicinity of the posterior depression. With the exception of *Krithe peypouqueti*, the mean length/height ratio of 1.58 is the lowest that we have recorded for a species of *Krithe* and gives this species an isolated position on scattergrams (Figs 19, 20). The vestibules of *Krithe* sp. 6 are very narrow, with the inner margin lying close and parallel to the outer margin. MS appear complex, with three small anterior scars and four adductors.

*Krithe* sp. 6 has a depth range of 1 662–2 916 m. The species is a minor component of the Lower *Krithe* Fauna, but is relatively more abundant in the Lower Bathyal Zone.

*Krithe* sp. 7

Figs 17E–F, 18J, 23A

*Illustrated material*

MF-0446, RV, TBD 6851, 2 916 m.

MF-0454, LV, TBD 6851, 2 916 m.

*Remarks*

A relatively large species with a mean length/height ratio of 1.89 (Fig. 20). In external lateral view, the species is characterized by a broadly rounded AM that contrasts with a somewhat extended PM, which in the RV has a small



re-entrant above the posterior depression. The DM is gently convex, which helps to distinguish it from *Krithe* sp. 4. The anterior inner lamella is moderately wide but the vestibule is small and almost rectangular in shape.

*Krithe* sp. 7 has a depth range 1 600–2 916 m. The species is a minor component of the Lower *Krithe* Fauna but is relatively more abundant in the Lower Bathyal Zone, particularly in the uppermost part.

*Krithe* sp. 19

Figs 17O–P, 18I, 23B

*Illustrated material*

MF-0447, RV, TBD 6851, 2 916 m.

*Remarks*

A small elongate species that has the highest mean length/height ratio within the *Krithe* populations that we studied (2,30—Figs 19, 20). In external lateral view, *Krithe* sp. 19 is characterized by prominent re-entrants in both valves, above the posterior depression, that give the valve a 'pleated' appearance. The anterior vestibules are small, and largely lie anterior to two lobes in the marginal zone. The anterior MS appears to consist of a cluster of three small scars.

*Krithe* sp. 19 has a depth range 1 662–2 916 m. Although it occurs in small numbers (maximum of 4% total ostracod fauna at TBD 6851), it is the second most abundant taxa of the Lower *Krithe* Fauna throughout most of the Lower Bathyal Zone (Fig. 13).

*Krithe* sp. 22

Figs 17Q–R, 18K, 22D

*Illustrated material*

MF-0448, RV, TBD 6851, 2 916 m.

MF-0458, LV, TBD 6851, 2 916 m.

*Remarks*

A small species with a gently rounded DM outline in lateral view. Its overall shape is very similar to that of *Krithe capensis* and the two have similar length/height ratios (*Krithe* sp. 22 = 1,93; *Krithe capensis* = 1,86). However, the great difference in size between the two species facilitates identification (Fig. 20). Internally, the two species differ in shape of the vestibule; in *Krithe* sp. 22 it is small, with a short, straight, inner margin post-adjacent to it.

*Krithe* sp. 22 is a rare abyssal form that we encountered only in sample 6851 (2 916 m), where it constitutes 12 per cent of the total *Krithe* population.

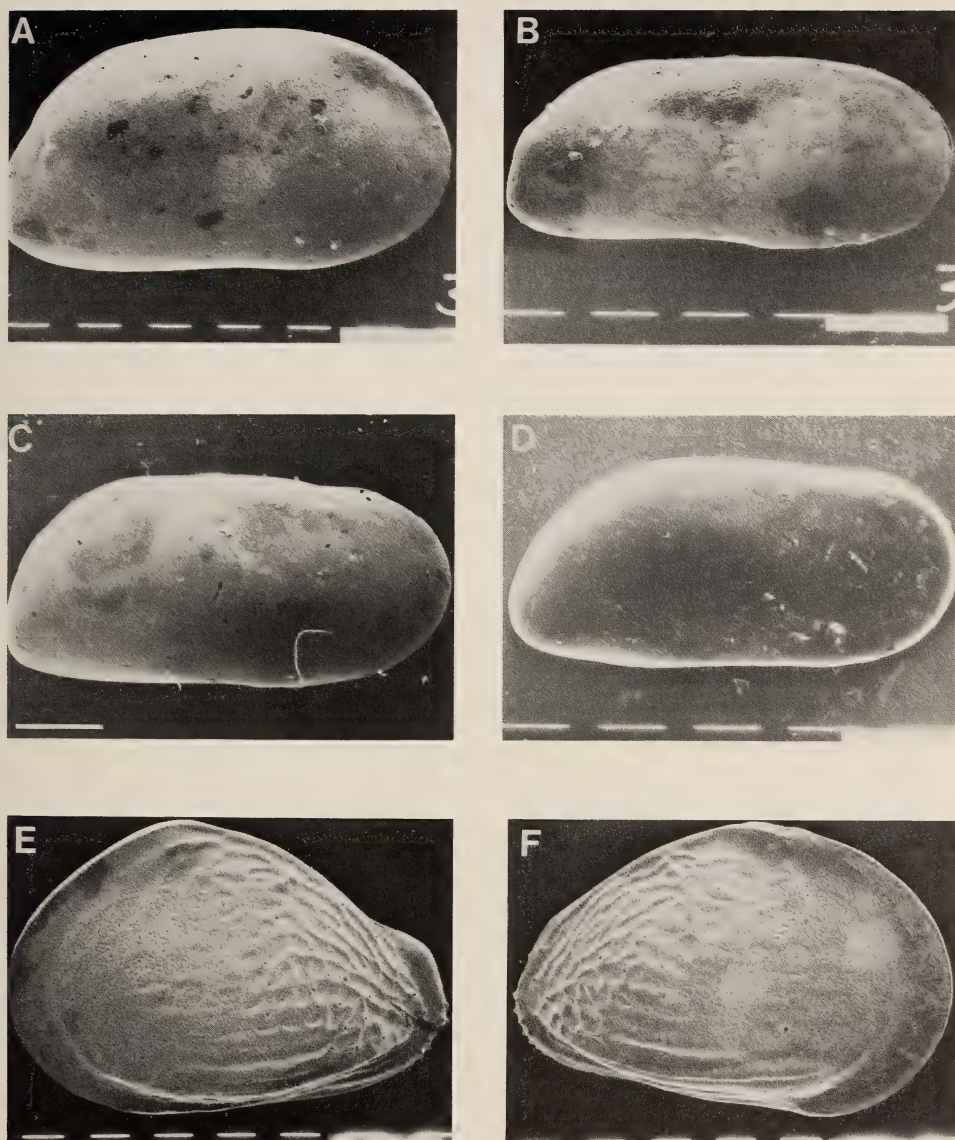


Fig. 23. A. *Krithe* sp. 7, SAM-PQ-MF-0446, RV, TBD 6851, 2 916 m. B. *Krithe* sp. 19, SAM-PQ-MF-0447, RV, TBD 6851, 2 916 m. C. *Krithe* sp. 9, SAM-PQ-MF-0443, RV, TBD 3524, 475 m. D. *Parakrithe* sp. 10, SAM-PQ-MF-0449, RV, TBD 3553, 1 003 m. E-F. *Buntonia rosenfeldi* sp. nov. TBD 3338, 990 m. E. SAM-PQ-MF-0460, LV, SEM 2799. F. SAM-PQ-MF-0459, holotype, RV, SEM 2792. Scale bars = 100 microns.



Genus *Parakrithe* van den Bold, 1958a*Parakrithe* sp. 10

Figs 17I, 18B, 23D

*Illustrated material*

MF-0449, RV, TBD 3553, 1 003 m.

*Remarks*

This relatively large (0,72 mm) species has a slight bulge on the antero-dorsal margin in lateral view, and a less pointed postero-ventral outline than in most of the examples discussed by Peypouquet (1979). The anterior vestibule is relatively large and widens anteriorly. We place it within Peypouquet's (1979) ecotype A3. Van den Bold (1966) illustrated three species of the genus from the Miocene of Gabon (*P. robusta* sp. nov., *P. datylomorpha* Ruggieri, 1962, and *P. vermunti* (van den Bold, 1946)), but none are conspecific with our species.

Off south-western Africa, *Parakrithe* sp. 10 has a depth range of 900–1 353 m, which limits it to the portion of the AAIW that lies between the base of the Salinity Minimum Zone, and the top of the NADW mass.

Family **Buntoniidae** Apostolescu, 1961Genus *Buntonia* Howe, 1935 (*in* Howe & Chambers, 1935)

Ruggieri (1958) split the genus *Buntonia* and separated off the large, relatively thin-shelled and smooth taxa into *Quasibuntonia*. Van Morkhoven (1963) did not accept this as taxonomically valid, and we follow his example. However, the forms that were represented in Ruggieri's *Quasibuntonia* certainly constitute a geographically well-defined group: they inhabit relatively deep water, and are (and were) confined to areas adjacent to Africa, and in the Mediterranean (Benson & Sylvester-Bradley 1971). Representatives of *Buntonia* s.s. have a world-wide distribution at all water depths.

The genus *Buntonia* is an important component of the ostracod populations off south-western Africa, where five species occur over a latitudinal range 17°S to 35°S, in water depths of 95–2 070 m (Fig. 24). All five species are found in the Neritic Zone, where mean values of the genus's abundance within the ostracod population (in samples that contain the genus) are 9,8 per cent (range 0,1–66%). Only two species (*B. rosenfeldi* sp. nov. and *Buntonia* sp. 34) extend beyond the continental shelf on to the slope, and only *B. rosenfeldi* sp. nov. occurs in the Bathyal Zone. The latter species belongs in the group *Quasibuntonia*, as understood by Ruggieri (1958) and Benson & Sylvester-Bradley (1971). We did not find the genus in the Abyssal Zone.

Despite the reduction in diversity of the genus into progressively deeper water, mean values of abundance in the Bathyal Zone are higher than in shallow-water areas: 30 per cent (range 3–100%). A three-point running mean



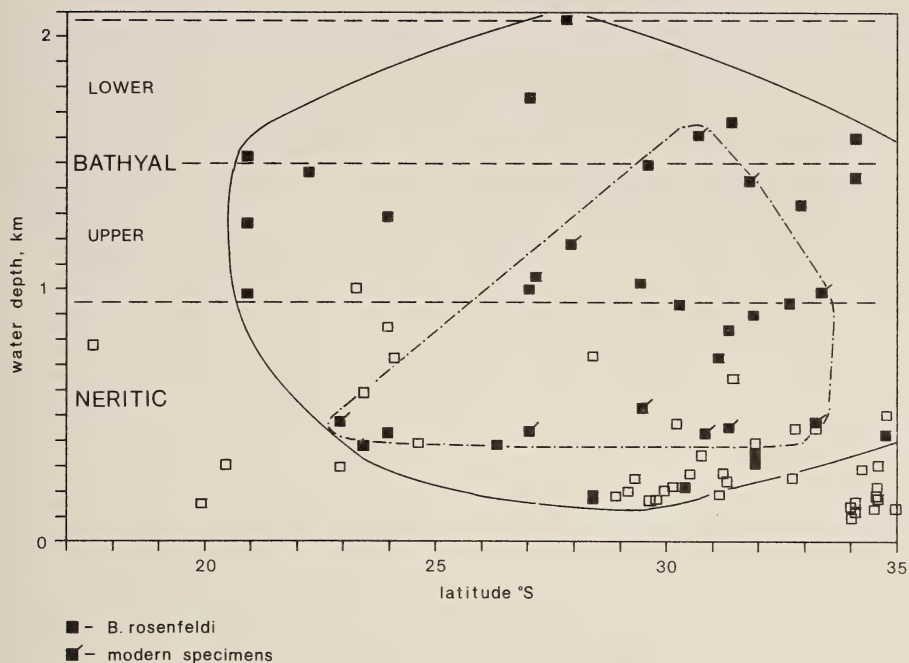


Fig. 24. Latitude and water depth of samples bearing *Buntonia* spp. Solid points and outline indicate the distribution of *Buntonia rosenfeldi* sp. nov.

plot of the percentage of all *Buntonia* species within the overall ostracod populations from all our samples off south-western Africa (Fig. 25) shows a general increase in abundance of the genus from the inner shelf to the lower part of the Neritic Zone (i.e. 95–900 m). We detect three populations within these shallow-water assemblages but will defer further discussion to a later publication. At the Neritic/Bathyal boundary (c. 950 m), there is fluctuation at the apex of the curve, which peaks at around 25 per cent of the overall ostracod population. Below this depth, in the Upper Bathyal Zone, values fall steadily for about 250 m. Clearly, there is an important physio-chemical barrier at around 950 m that has the following effects: (a) the disappearance of *Buntonia* sp. 34; (b) a reduction in the relative size of the population of *B. rosenfeldi* sp. nov.

*Buntonia rosenfeldi* sp. nov. is the only bathyal species of the genus, although valves of *Buntonia* sp. 34 occur as deep as 1 050 m. Mean values of percentage of the ostracod population show a high in the Upper Bathyal Zone compared to the Lower Bathyal Zone (35%, range 6–100%; 20%, range 3–40%, respectively), but these figures hide the true distribution, which is closely linked to the boundary zones of the water masses. We will discuss this under 'Remarks' on *B. rosenfeldi* sp. nov.

Peypouquet & Benson (1980) recorded the genus (as *Quasibuntonia* spp.) from their transects in the Cape and Angola basins. There are too few data points on their curves to make a detailed comparison with our results (cf. Figs 25, 26), but they suggest a decline from high values of percentage of overall ostracod populations in shallow water (20% in 450 m) to a low of 1 per cent at around 1 000 m. They recorded three sites with relatively high values (20–30%) in depths that we classify as Lower Bathyal/uppermost Abyssal, and a deeper site (2 800 m) at 6 per cent. These data are broadly compatible with our results, but we suspect that they are too scattered to resolve the actual distribution.

Benson & Sylvester-Bradley (1971) discussed the distribution of the related, relatively large species, *B. sulcifera* (Brady, 1887) and *B. radiatopora* (Seguenza, 1880), and concluded that these deep-water buntoniids represent the remnants of a 'Tethyan' fauna that is restricted to a circum-Africa zone.

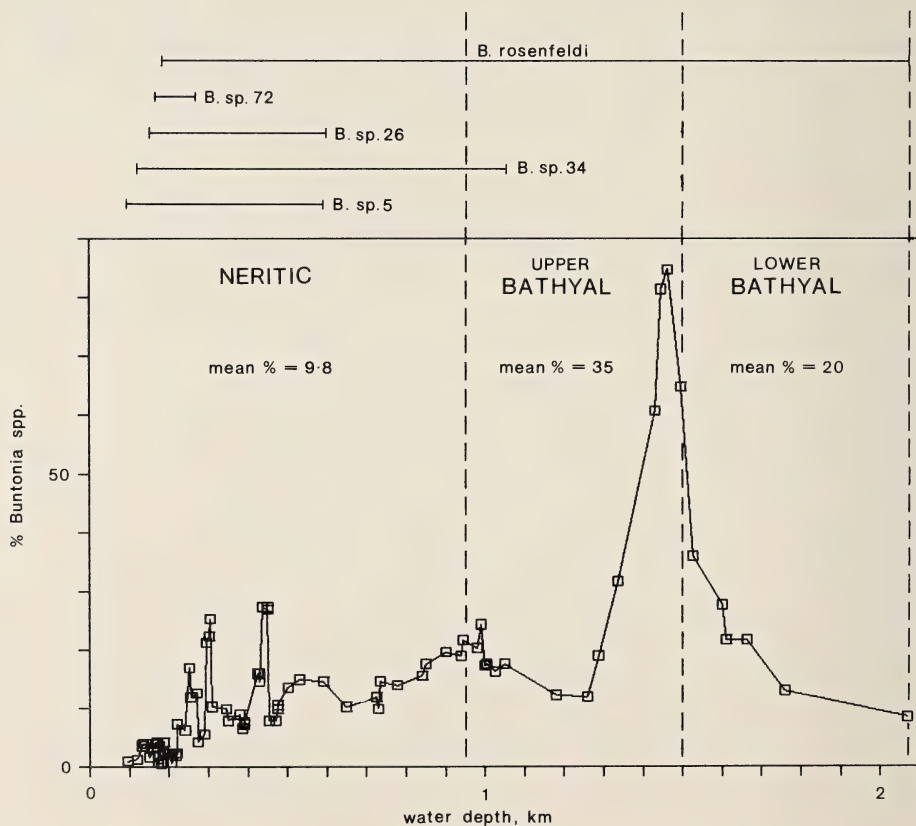


Fig. 25. *Buntonia* species as percentage of total ostracod fauna plotted against water depth. Values are five point running means. Depth ranges for all *Buntonia* species on the continental margin are shown by bars. Mean % = mean percentages of *Buntonia* species in total ostracod fauna for each depth zone.

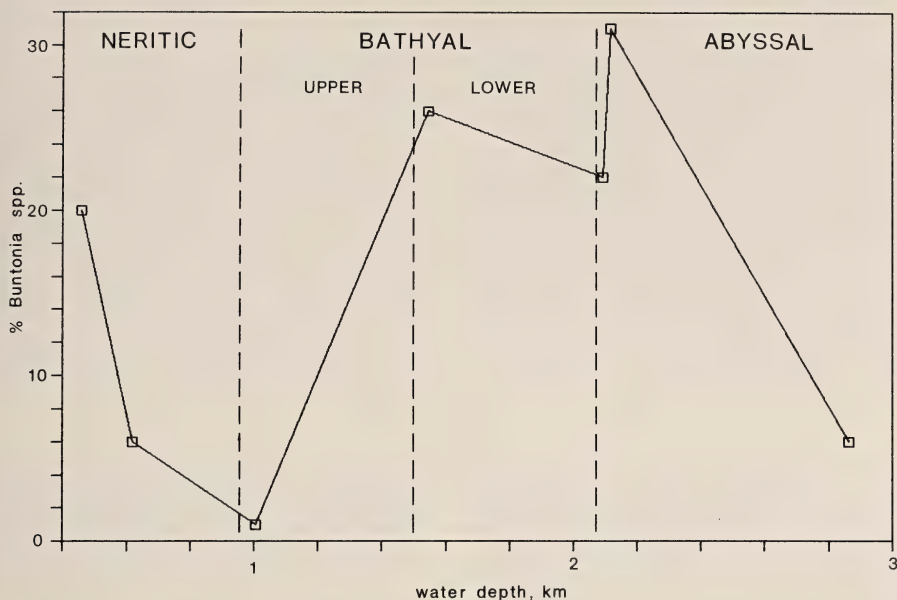


Fig. 26. *Buntonia* species as percentage of total ostracod fauna plotted against water depth for a profile off Walvis Bay. Data computed from Peypouquet & Benson (1980).

Neither Cronin (1983) nor Benson *et al.* (1983) recorded taxa from the continental margin of eastern North America that would fall into the category *Quasibuntonia*.

***Buntonia rosenfeldi* sp. nov.**

Figs 23E–F, 27A–D

*Buntonia sulcifera*? (Brady, 1887) Rosenfeld & Bein, 1978: 18, pl. 1 (fig. 21).

*Buntonia* sp. 1 Boomer, 1985: 34–35, pl. 2 (figs 27–28). (These are probably all juveniles.)

*Buntonia* sp. 2 Boomer, 1985: 35–36, pl. 2 (figs 33–34). (These are probably all adults.)

*Derivation of name*

The species is named for Dr A. Rosenfeld (Geological Survey of Israel) for his work on deep-water ostracods from north-western Africa.

*Holotype*

MF-0459, RV, TBD 3338, 990 m.

*Paratypes*

MF-0460, LV, TBD 3338, 990 m.

MF-0461, LV, TBD 3338, 990 m.

MF-0462, RV, TBD 3109, 900 m.



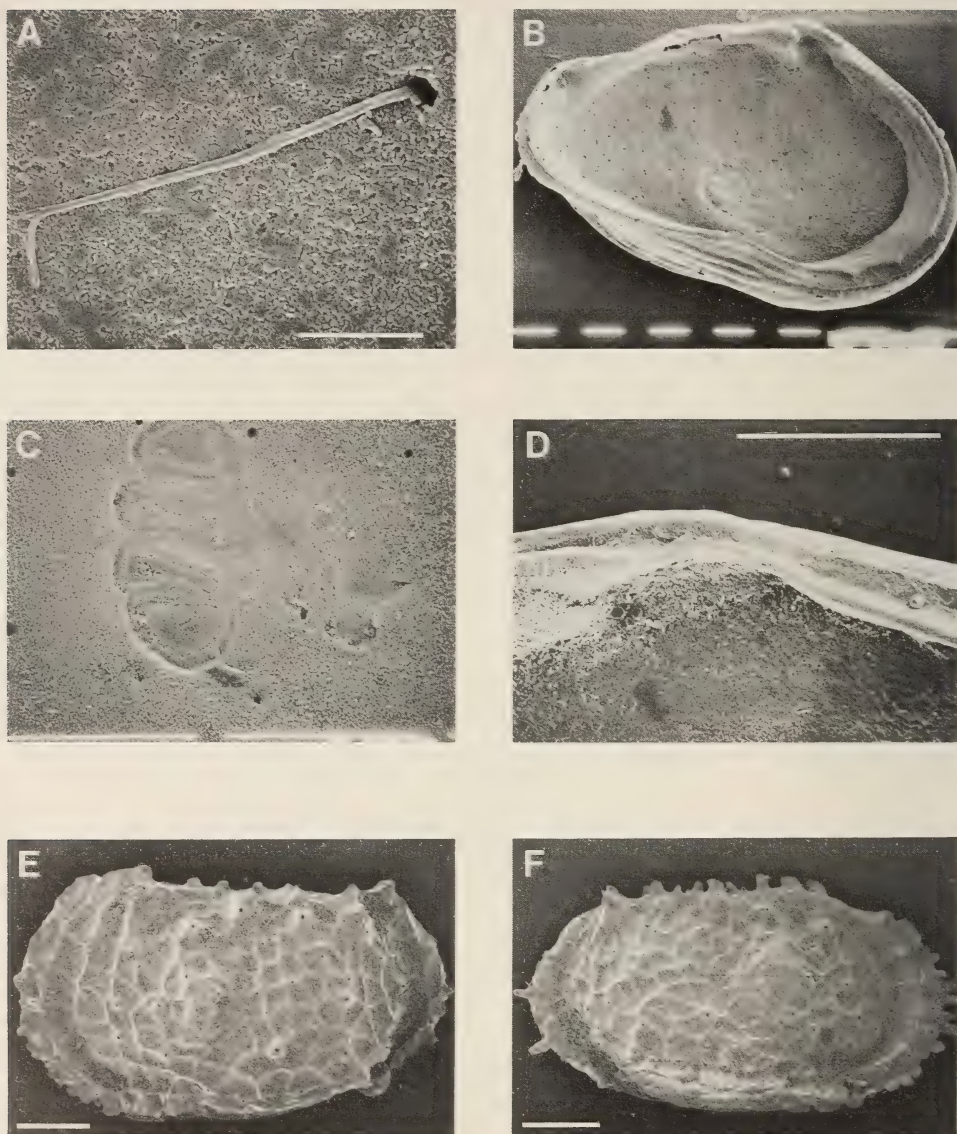


Fig. 27. A-D. *Buntonia rosenfeldi* sp. nov. A-C. TBD 3338, 990 m. A. SAM-PQ-MF-0459, holotype, LV seta, SEM 2793. B. SAM-PQ-MF-0461, LV internal view, SEM 2795. C. SAM-PQ-MF-0461, LV, MS, SEM 2796. D. SAM-PQ-MF-0462, RV, TBD 3109, 900 m, SEM 2790. E-F. *Dutoitella suhmi* (Brady 1880), TBD 6851, 2 916 m. E. SAM-PQ-MF-0463, LV, SEM 2936. F. SAM-PQ-MF-0464, RV, SEM 2940. Scale bars: A = 10 microns; C-F = 100 microns.

### Diagnosis

Species with well-developed longitudinal ventro-lateral keel and reticulate ornamentation in posterior part of lateral valve surface.

### Description

Typical ovate buntoniid in lateral outline with broadly rounded AM and narrow, bluntly truncated PM. High, arched DM that has an abrupt step to the PM in LV, but is continuous with PM outline in RV. VM is straight or slightly concave. There is a prominent, keeled, ventro-lateral ridge that passes anteriorly into a faint rib running parallel to the AM. AM area is strongly compressed. Posterior lateral surface is reticulate, with indistinct longitudinal ribbing and prominent conjugate pores. Anterior valve surface is faintly reticulate, with a delicate tracery of muri and inter-mural pitting.

Hinge is amphidont, with both ATE in LV open ventrally. There are narrow anterior vestibules. MS consist of four adductors, the ventral and dorsal of which are ovate, and a hooked anterior scar, above which lie two small rounded scars.

### Dimensions (mm)

	length	height
MF-0459	0,66	0,43
MF-0460	0,69	0,45
MF-0461	0,68	0,46
MF-0462	0,67	0,44

### Remarks

Three species are closely related to *B. rosenfeldi* sp. nov.: *B. radiatopora* (Seguenza, 1880), *B. pyriformis* (Brady, 1880), and *B. sulcifera* (Brady, 1887).

The closest is *B. radiatopora* (Seguenza, 1880) from the Neogene of southern Italy. Seguenza (1880) recognized two varieties, but stated that there is a continuous transition between them and that he was unable to differentiate separate species. *Buntonia radiatopora radiatopora* has longitudinal ridges in the posterior half of the valves, whereas the variety *B. r. sculpta* has ridges over the whole valve surface. The former variety has been illustrated by Benson & Sylvester-Bradley (1971), and both varieties by Colalongo (1965). *Buntonia rosenfeldi* sp. nov. differs from *B. radiatopora* (Seguenza) in having reticulate ornamentation in the posterior half of the valve.

*Buntonia sulcifera* (Brady, 1887) is very close to *B. radiatopora* (Seguenza), because both species possess ornamentation of longitudinal ribs in the posterior half of the valve. They may be conspecific, although the rib pattern in the former may be sharper if the illustration by Benson & Sylvester-Bradley (1971) of a specimen from the Mozambique Channel is the same species as Brady's. Whatever the case, *B. rosenfeldi* differs from *B. sulcifera* by lacking the longitudinal median ribs in the posterior half of the valve.

*Buntonia pyriformis* (= *B. mackenziei* nom. nov. Puri & Hulings, 1976) has a similar outline to *B. rosenfeldi* but is more elongate, has a smooth lateral valve surface (Brady 1880: 78), and an eyespot (Puri & Hulings 1976: 281).

*Buntonia rosenfeldi* sp. nov. occurs over a depth range of 186–2 070 m off south-western Africa, and 1 418–2 859 m off north-western Africa (recorded as *B. sulcifera*? by Rosenfeld & Bein 1978, fig. 21). *Buntonia radiatopora* is reported as living at 2 816 m in the eastern Mediterranean and fossil in the Plio–Pleistocene of southern Italy and Sicily (Benson & Sylvester-Bradley 1971). *Buntonia sulcifera* (Brady, 1887) was recorded by Brady (1887) from 3 655 m off Mauritius, and 2 980 m from the Mozambique Channel by Benson & Sylvester-Bradley (1971), and *B. pyriformis* (Brady, 1880) was first recorded in 675 fm (1 234 m) off Brazil (Brady 1880—'Challenger' site 120), and has been found between 400 m and 830 m off north-western Africa by Rosenfeld & Bein (1978). *Buntonia* cf. *B. pyriformis* (Brady) (recorded as cf. *B. mackenziei* Puri & Hulings) has been reported from late Miocene and late Pliocene strata at DSDP site 608 in the North Atlantic by Whatley & Coles (1987).

Figure 28 shows the abundance of *Buntonia rosenfeldi* sp. nov. across its depth range off south-western Africa. In the Neritic Zone it constitutes a mean

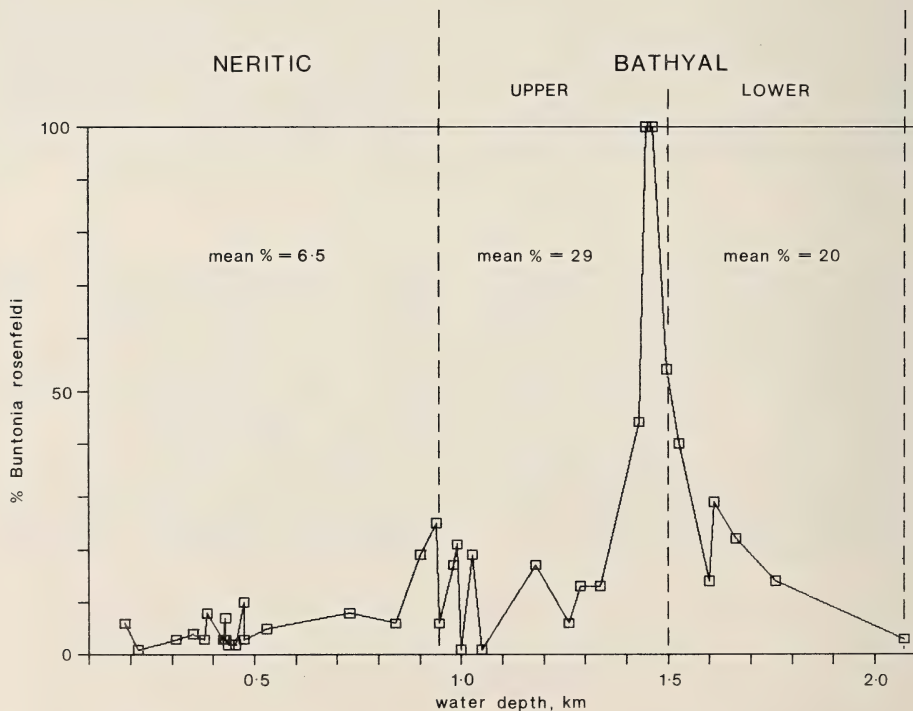


Fig. 28. *Buntonia rosenfeldi* sp. nov. as percentage of total ostracod fauna plotted against water depth. Values have not been smoothed.



of 6.5 per cent (range 1–25%) the ostracod population (in samples in which it occurs) and, for depths shallower than approximately 900 m, there are few samples with values above 10 per cent, although there is a slow, progressive increase with depth. Within the Bathyal Zone (i.e. 950–2 070 m), the mean abundance of *B. rosenfeldi* is 27 per cent (range 1–100%), so that it appears to represent a characteristic element of the deep-water fauna. However, it is at water mass boundaries that the species is most successful in establishing itself: at the Neritic/Upper Bathyal boundary values are c. 20 per cent, and at the Upper/Lower Bathyal boundary values are over 35 per cent. Nevertheless, we did not record it from the Abyssal Zone, and values in the Lower Bathyal Zone steadily decline below about 1 600 m. From these data we conclude that *B. rosenfeldi* prefers relatively cold, saline water, and that it is particularly successful, in comparison with other ostracod species, at tolerating the unstable conditions that occur at the major water mass boundaries (i.e. at the base of the AAIW low salinity zone, and the AAIW/NADW shear zone). It cannot tolerate the adverse conditions of the AABW.

Family **Trachyleberididae** Sylvester-Bradley, 1948

Subfamily Unicapellinae Dingle, 1981

Genus *Dutoitella* Dingle, 1981

Recognition of this genus in Quaternary deep-sea sediments in the south-eastern Atlantic necessitates expansion of the concept of this genus to include reticulate species. This in turn allows the accommodation within *Dutoitella* of several species of previously uncertain affinity: *D. eocenica* (Benson, 1977) from the South Atlantic, '*Suhmicythere*' sp. Benson *et al.*, 1983, from the north-western Atlantic, and *D. crassinodosa* (Guernet, 1985) from the Indian Ocean. Phylogenetic implications of these new data are that, between Maastrichtian and Eocene times, the genus migrated from south-eastern African outer continental-shelf environments into deeper-water habitats on both sides of the South Atlantic and in the Indian Ocean. There was a concomitant development of reticulation.

A similar trend can be seen in *Atlanticythere*, with spinose species appearing by Eocene times. Architectural similarity between the two genera strongly suggests a common ancestor (Fig. 29).

*Dutoitella suhmi* (Brady, 1880)

Figs 27E–F, 30A–B, 31A, C, F

*Cythere suhmi* Brady, 1880: 106–107, pl. 26 (fig. 3a–h). Puri & Hulings, 1976: 290–291, pl. 17 (figs 7–12), text-fig. 10.

'*Suhmicythere*' *suhmi* (Brady, 1880): Whatley & Coles, 1987, pl. 6 (figs 18–21).

'*Suhmicythere*' sp. Benson *et al.*, 1983, pl. 1 (fig. 8).



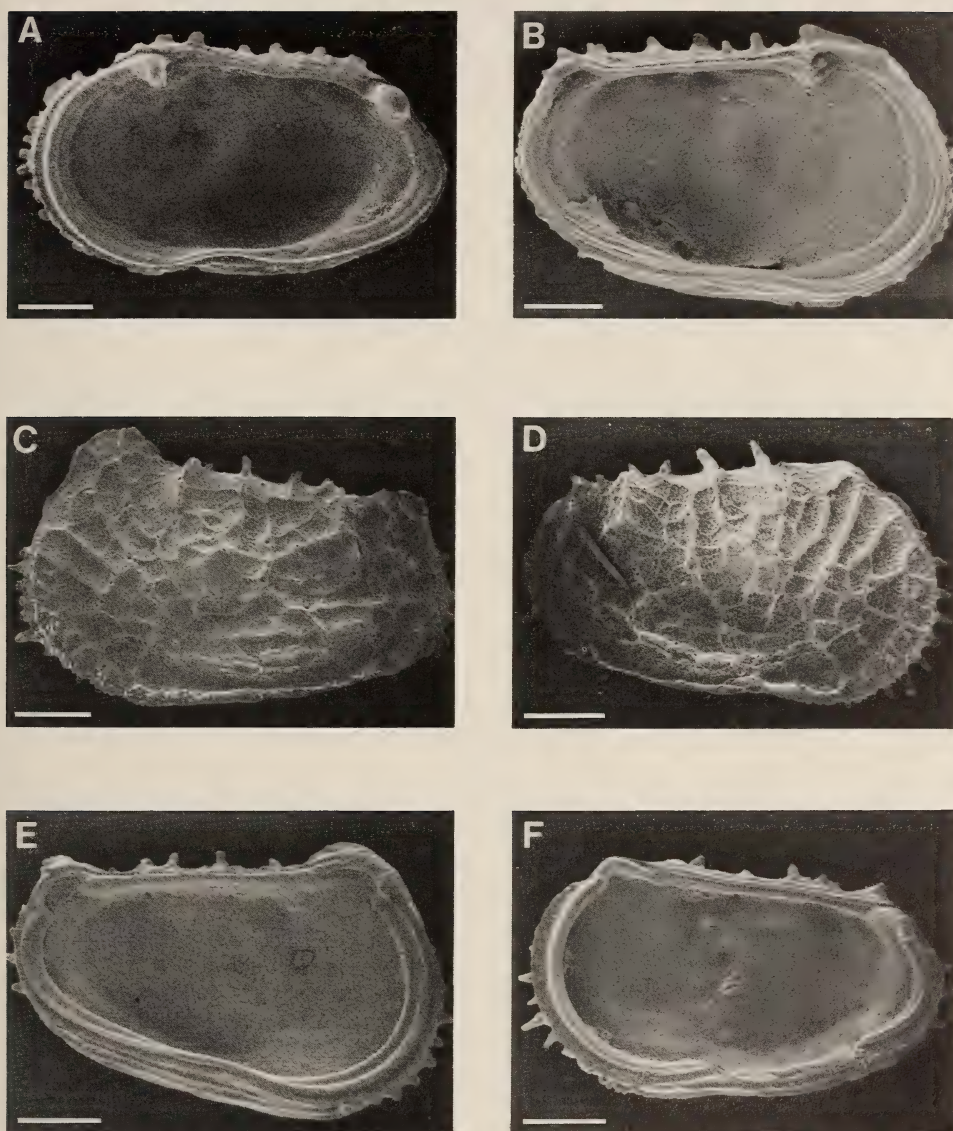


Fig. 30. A-B. *Dutoitella suhmi* (Brady, 1880), TBD 6851, 2 916 m. A. SAM-PQ-MF-0465, RV internal view, SEM 2942. B. SAM-PQ-MF-0466, LV internal view, SEM 2938. C-F. *Abyssocythere australis* Benson, 1971, TBD 6851, 2 916 m. C. SAM-PQ-MF-0467, LV, SEM 2946. D. SAM-PQ-MF-0468, RV, SEM 2960. E. SAM-PQ-MF-0469, LV internal view, SEM 2948. F. SAM-PQ-MF-0470, RV internal view, SEM 2957.

Scale bars = 100 microns.



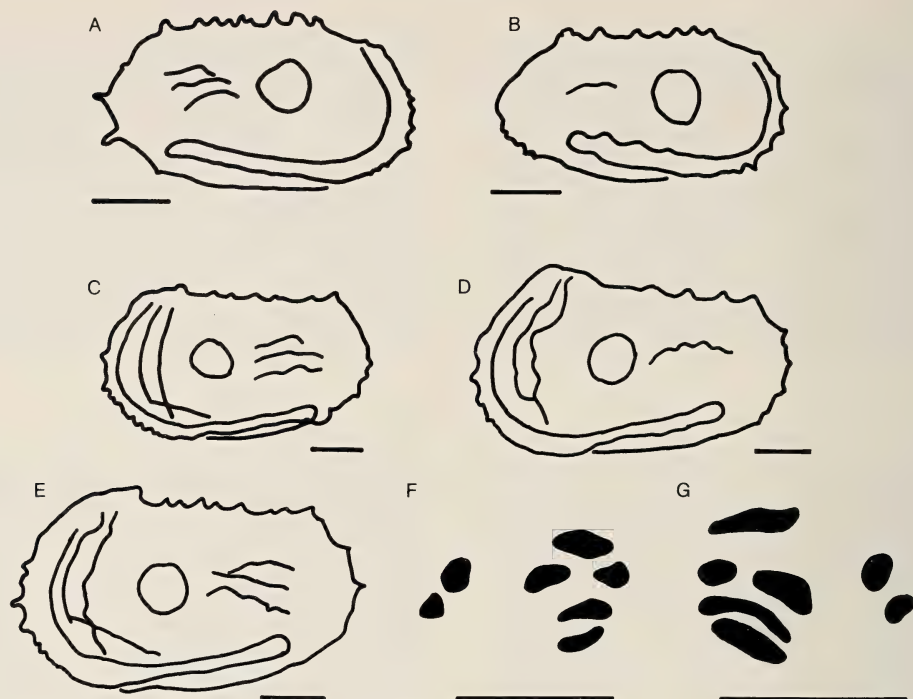


Fig. 31. Comparative morphology of various species of *Dutoitella*. A. *D. suhmi* (Brady 1880), SAM-PQ-MF-0464, RV, TBD 6851, 2 916 m, SEM 2940. B. *D. mimica* Dingle, 1981, SAM-K5748, RV, TBD 818, Alaphard Formation, Agulhas Bank, Maastrichtian III. C. *D. suhmi* (Brady 1880), SAM-PQ-MF-0463, LV, TBD 6851, 2 916 m, SEM 2936. D. *D. neogenica* (Benson 1977), USNM 190300, LV, DSDP site 22, Lower Miocene, from Benson (1977, pl. 1 (fig. 8)). E. '*Suhmicythere*' sp., USNM 247710, 3 000 m off Newfoundland, Quaternary, from Benson *et al.* (1983, pl. 1 (fig. 8)); is probably conspecific with *D. suhmi* (Brady, 1880). F. MS of *D. suhmi* (Brady, 1880), SAM-PQ-MF-0465, RV, TBD 6851, 2 916 m, SEM 2944. G. MS of *D. mimica* Dingle, 1981, SAM-K5449, LV, TBD 818, Alaphard Formation, Agulhas Bank, Maastrichtian III. Scale bars = 100 microns.

outline, with contrasting eared LV and stepped RV antero-dorsal outline, of the Cretaceous (Campanian–Maastrichtian) type species (*D. dutoiti* Dingle, 1981). Its MS pattern is very similar to that of *D. mimica* Dingle, 1981 (Santonian–Maastrichtian). *Dutoitella suhmi* (Brady) differs from both Cretaceous species in being reticulate, having a less prominent SCT, and having the lateral ridge or node post-adjacent to the SCT replaced by three short, indistinct ribs. With the exception of the reticulation, the surface architecture, including location of pore conuli and dorsal margin spines of *D. suhmi* (Brady) and *D. mimica*, is very similar (Fig. 31). The internal features of these two species are also very close, the major difference being that the LV PTE of *D. suhmi* lies in a slightly more postero-ventral position.

The illustrations of Puri & Hulings (1976: 290–291, pl. 17 (figs 7–12), text-fig. 10) of lectotypes of *D. suhmi* (Brady) show a slightly different MS pattern to our specimens of both *D. suhmi* (Brady) and *D. mimica* Dingle, 1981. The former show four non-divided adductors, whereas our specimens have a sub-divided second adductor. R. C. Whatley (pers. comm. 1988) informs us, however, that this variation in *D. suhmi* is within the range that he has observed for the species worldwide, and appears to have no taxonomic significance.

Brady (1880) reported *Cythere suhmi* from water depths of 100–4 600 m, and Whatley & Coles (1987) have found it in deep-water (>3 000 m) Miocene–Quaternary sediments of the North Atlantic. *Dutoitella suhmi* (Brady, 1880) is known from site TBD 6851 within the Abyssal Zone (2 916 m) of the Cape Basin, where it forms 6 per cent of the ostracod fauna.

Benson *et al.*'s (1983) record of '*Suhmicythere*' sp. from 3 000 m on the continental slope off Newfoundland also probably refers to this species, and it is possible that Peypouquet & Benson's (1980) citation of '*Shumicythere*' [sic] from a range of 3 797–4 595 m in the Angola Basin at least refers to species of *Dutoitella*. Benson (1977) listed '*Suhmicythere*' sp. from late and mid-Miocene horizons at DSDP site 357 on the Rio Grande Rise, but did not illustrate the material. These may, therefore, also be records of reticulate species of *Dutoitella*.

When he originally erected the two species *Atlanticythere? eocenica* Benson and *A.? neogenica* Benson, Benson (1977: 877) queried their generic assignment: 'This species [*A.? eocenica*] and *A.? neogenica* Benson, n. sp. may be considered later as generically distinct [from other species of *Atlanticythere*].' The continuous AM and ventro-lateral ridge indicates that Benson's species belong in *Dutoitella*. In addition, we consider that these two species are conspecific and, in revision, designate *D. eocenica* (Benson, 1977) to be the valid taxon, because it is described earlier in the publication (i.e. *D. neogenica* (Benson, 1977) is a junior synonym of *D. eocenica* (Benson, 1977)).

The species *D. eocenica* (Benson, 1977) and *D. suhmi* (Brady) have very similar patterns of surface reticulation, with the main points of difference being in the routes of the reticulation muri adjacent to the AM, and the presence of a short ridge post-adjacent to the SCT in *D. eocenica* compared to three narrow ribs in *D. suhmi*. In this latter feature, *D. eocenica* is close to the Cretaceous species of the genus (Fig. 31).

We also refer '*Cythereis*' *crassinodosa* Guernet, 1985, to *Dutoitella* and consider it to be another close relative of *D. suhmi*. Guernet (1985) compared his species generically to '*Suhmicythere*' sp. Benson *et al.*, 1983, and recorded it from bathyal assemblages of early (Ypresian) to late (Priabonian) Eocene age at DSDP site 214 (Chagos Ridge). He also mentioned 'C.' aff. *C. crassinodosa* from the Lower Eocene at DSDP site 245 (Madagascar Basin, south-western Indian Ocean), and 'C.' cf. *C. crassinodosa* from the middle Eocene at DSDP site 214 on the central 90 East Ridge. *Dutoitella crassinodosa* (Guernet, 1985)

differs from *D. suhmi* (Brady) in having a more prominent SCT and prominent nodes on its DM and VM.

Phylogenetic implications of our new data are summarized in Figure 29 and suggest that in the early Tertiary, *D. mimica* migrated from its preferred habitats on the outer continental shelf (?100–200 m water depths—see Dingle 1981, 1985) and colonized deep-water sites in the western South Atlantic and in the south-western, north-western and central Indian Ocean. During the course of this, mutation into at least two species occurred: *D. eocenica* (Eocene–Miocene) and *D. crassinodosa* (Eocene). Subsequent development produced *D. suhmi* (Miocene–Quaternary) and possibly other species that have been recorded as '*Suhmicythere*' (e.g. Benson 1977; Peypouquet & Benson 1980).

At this stage it is premature to speculate on possible links between *Dutoitella* and *Atlanticythere* but, if the latter did evolve from the former, then the main architectural modifications necessary before Maastrichtian time were the re-organization of the route of the AM and ventro-lateral ridges, a reduction in the size of the SCT and post-adjacent nodes and ridges, and a general increase in valve size. So far, the only record of the genus *Atlanticythere* in the eastern South Atlantic is *Atlanticythere* sp. B058 from the Eocene of the Agulhas Bank (Frewin 1987).

Neither Rosenfeld & Bein (1978) nor Cronin (1983), in their studies of deep-water faunas, referred species to the genera *Dutoitella*, *Atlanticythere*, or '*Suhmicythere*'.

#### Subfamily Trachyleberidinae Sylvester-Bradley, 1948

##### Genus *Abyssocythere* Benson, 1971

##### *Abyssocythere australis* Benson, 1971

Figs 30C–F, 32A

*Abyssocythere australis* Benson, 1971: 18, pl. 3 (fig. 7), text-fig. 12.

##### *Illustrated specimens*

MF-0467, LV, TBD 6851, 2 916 m.

MF-0468, RV, TBD 6851, 2 916 m.

MF-0469, LV, TBD 6851, 2 916 m.

MF-0470, RV, TBD 6851, 2 916 m.

##### *Remarks*

Externally, the specimens from off south-western Africa differ from those off southern Australia only by possessing a slightly weaker AM rim. In his original description of *A. australis*, Benson (1971) did not give details of the internal features of the species, but we can report that the MS pattern (Fig. 32) is similar to that of the type species *A. casca* Benson, 1971. Also, the hinges of the two



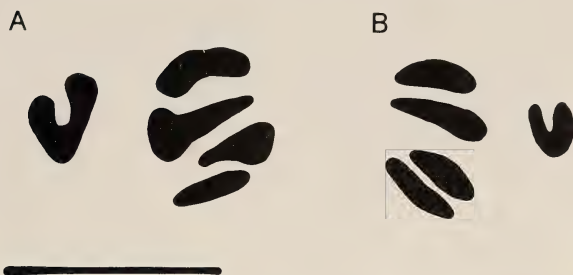


Fig. 32. MS of *Abyssocythere*. A. *A. australis* Benson, 1971, SAM-PQ-MF-0470, RV, TBD 6851, 2 916 m, SEM 2958. Scale bar = 100 microns. B. *A. casca* Benson, 1971, no locality given, c. 3 000 m, off Madagascar (from Benson 1971, fig. 6). No scale given.

species are similar but, in comparison with *A. casca*, our material exhibits a weaker ATE in the RV, where the anterior tooth is more elongate and in lateral view projects above the valve margin at the ACA. In addition, the socket at the anterior end of the narrow ME groove is small and does not project below the general line of the hinge, as occurs in *A. casca*.

When he originally proposed the genus, Benson (1971) recorded six species of *Abyssocythere*, all of which had modern representatives. Subsequently, four more have been reported in the literature, with the result that ten separate species are now known, six of which have a fossil record that ranges Eocene to Recent (Table 3).

Figure 33 shows the distribution of the Quaternary species of *Abyssocythere*. Our new data pose an interesting problem in that the geographical range of *A. australis* can now be extended across the Southern Ocean into the Cape Basin, but that the range of *A. casca* seems to be limited to the northern Mozambique/Somali basins. The species have overlapping depth ranges (Table 3), so presumably there is a physico-chemical barrier to the migration of *A. casca* southward through the deep-water passages into the Cape Basin, although the nature of this barrier is not obvious, particularly in view of the fact that another of the typical Abyssal Zone taxa (*Poseidonamicus major*) does extend from the Mozambique Basin into the South Atlantic.

This species is a characteristic element of the Abyssal Zone ostracod assemblage. Our specimens were recovered from a single station (TBD 6851) at 2 916 m, where *Abyssocythere australis* constituted 6 per cent (23 valves) of the total ostracod fauna, with 17 per cent of the specimens considered modern. At the only previously known site (3 390 m, south of Australia), none of the specimens were modern (i.e. they were 'relict', presumably Pleistocene) (Benson 1971).

No representatives of the genus *Abyssocythere* were recovered from the deep-water surveys of Rosenfeld & Bein (1978), Peypouquet & Benson (1980), Benson *et al.* (1983), and Cronin (1983).

TABLE 3. Distribution of *Abyssocythere* species.

Species	Reference	Locality	Age	Depth range (m)
(a) Quaternary				
<i>Abyssocythere japonica</i> Benson, 1971	Benson (1971)	Pacific W Atlantic		3 400–3 766
<i>Abyssocythere</i> aff. <i>trinidadensis</i> (van den Bold, 1957a)	Benson (1971)			1 005
<i>Abyssocythere pannucea</i> Benson, 1971	Benson (1971)	Pacific Atlantic SW Indian S Australia SE Atlantic		2 089–3 292
<i>Abyssocythere atlantica</i> Benson, 1971	Benson (1971)			2 723–4 120
<i>Abyssocythere casca</i> Benson, 1971	Benson (1971)			1 605–3 850
<i>Abyssocythere australis</i> Benson, 1971	Benson (1971) this paper			2 916–3 390
(b) Fossil				
<i>Abyssocythere trinidadensis</i> (van den Bold, 1957a)	Benson (1971)	Caribbean	Eocene–Miocene	
<i>Abyssocythere atlantica</i> Benson, 1971	Benson (1971)	Atlantic (DSDP 12c)	Pliocene	
	Whatley & Coles (1987)	Atlantic (DSDP 606)	Pliocene	
	Benson (1974)	Indian (DSDP 237)	Upper Eocene	
<i>Abyssocythere</i> sp.	Benson & Peypouquet (1983)	Atlantic (DSDP 516)	Pliocene–Pleistocene	
<i>Abyssocythere</i> sp.	Benson & Peypouquet (1983)	Atlantic (DSDP 517)	Lower Pliocene	
<i>Abyssocythere braziliensis</i> Benson, 1983	Benson & Peypouquet (1983)	Atlantic (DSDP 518)	Upper Miocene	

DSDP 12c—Cape Verde Islands; DSDP 237—Seychelles Bank; DSDP 516—Rio Grande Rise; DSDP 517—Vema Channel; DSDP 518—Sao Paulo Plateau; DSDP 606—Central North Atlantic.



Fig. 33. Distribution of modern species of *Abyssocythere*. Re-plotted from data in Benson (1971—dots), with sample site TBD 6851 off south-western Africa shown as an open circle.

#### Genus *Ambocythere* van den Bold, 1958b

A listing of Recent species of this genus that have previously been described from relatively deep water, shows that the genus *Ambocythere* has a depth range from the inner continental shelf to the Abyssal Zone:

##### Bathyal/Abyssal

*A. ramosa*—Iceland, c. 1 000 m (Van den Bold 1965); Newfoundland, 2 938–3 210 m (Benson *et al.* 1983).

*Ambocythere* cf. *A. ramosa*—north Atlantic, 2 445 m (DSDP site 610, Whatley & Coles 1987).

*Ambocythere* sp. 3057—south-eastern Atlantic, 2 070 m (present study).

*Ambocythere caudata*—Iceland, c. 1 000 m (Van den Bold 1965).

##### Neritic

*Ambocythere keiji*—Venezuela, continental shelf (Van den Bold 1958b)

*Ambocythere stolonifera*—False Bay, South Africa, 30–40 m (Brady 1880)

*Ambocythere* spp. A, B, and C—south-eastern USA, 261–1 034 m (Cronin 1983).



Including fossil records, the genus has a Neogene range that includes the Caribbean, North and South Atlantic, Indonesia, Japan, Australia, and South Africa (Van den Bold 1965; Benson 1983).

*Ambocythere* sp. 3057

Figs 34A, 35A

*Illustrated specimen*

MF-0471, LV, TBD 3355, 2 070 m.

*Remarks*

This is a new species, but we have insufficient material (2 juveniles) to warrant a formal description. It was originally noted (but not described or illustrated) by Boomer (1985: 66) as *Ambocythere* cf. *A. stolonifera*, but its closest relative is *A. subreticulata* van den Bold, 1958b, from the Oligocene–Miocene of the Caribbean. *Ambocythere* sp. 3057 and *A. subreticulata* differ in the pattern and number of lateral ribs: *A. subreticulata* has numerous small riblets in the ventro-lateral area. *Ambocythere stolonifera* (Brady, 1880) from False Bay has a similar lateral outline and main rib arrangement to *Ambocythere* sp. 3057, but is more elongate and has several small ancillary riblets between the main dorsal and median ribs. The two other known deep-water species differ in the following points: *A. ramosa* is elongate, with numerous fine longitudinal ribs and a VM–AM–DM rim that is complete; *A. caudata* is also more elongate and has a marked re-entrant on the postero-ventral margin.

*Ambocythere* sp. 3057 is a rare species that has been recorded only from the Lower Bathyal/Abyssal Zone boundary off south-western Africa (TBD 3355, 2 070 m), where it constitutes 7 per cent of the total ostracod fauna. This value compares to a mean of 8,5 per cent of the total ostracod fauna at the two abyssal sites off Newfoundland for *Ambocythere ramosa* (Benson *et al.* 1983).

The wide sector of continental margin off south-western Africa that separates the sample site with *Ambocythere* sp. 3057 from the False Bay population of *Ambocythere stolonifera*, recorded by Brady (1880), is devoid of any record of the genus, so it is reasonable to assume that the deep- and shallow-water populations of *Ambocythere* in this region have a long history of genetic isolation. The only known possible record of the genus in the Tertiary of southern Africa is from the Agulhas Bank (TBD 819; Middle Eocene–Middle Oligocene), where Frewin's (1987) Indeterminate Genus 10 sp. B298 bears some resemblance to *A. stolonifera*.

Genus *Echinocythereis* Puri, 1954

This genus is distinguished from *Henryhowella* primarily on the possession of a split anterior MS. On this basis, the taxonomic position of several species

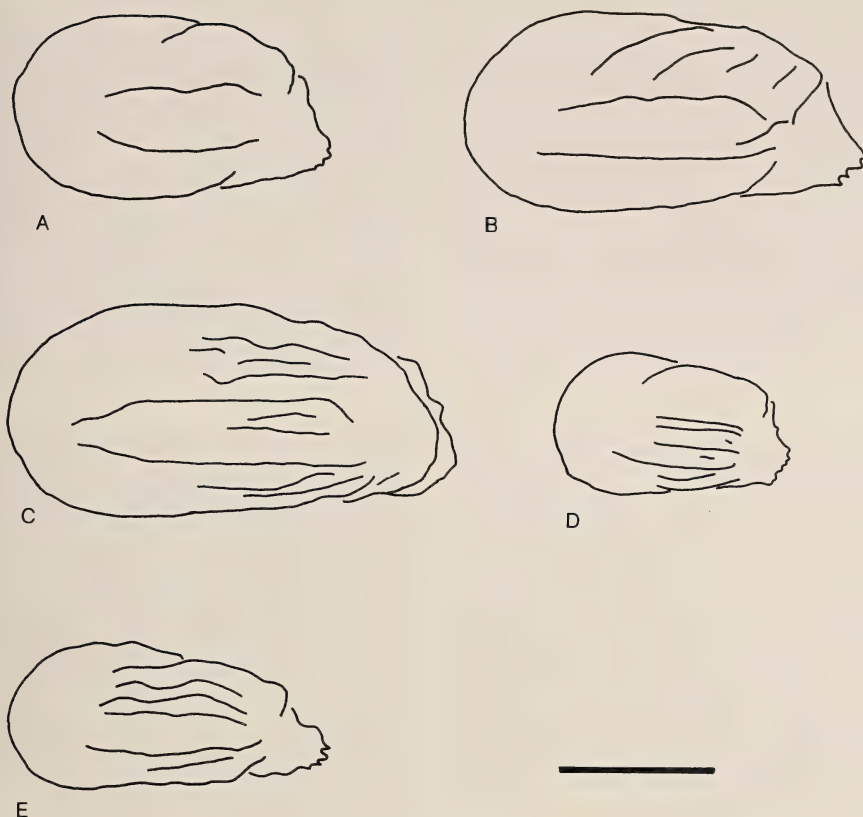


Fig. 34. Outlines of various species of *Ambocythere*. A. *Ambocythere* sp. 3057, SAM-PQ-MF-0471, LV, TBD 3355, 2 070 m. B. *A. subreticulata* van den Bold, 1958b, Miocene, Cuba (from Van den Bold 1958b, fig. 15). C. *A. stolonifera* (Brady, 1880), 'Challenger' station 140, 15-20 fm, False Bay (from Brady 1880, pl. 21 (fig. 3a)). D. *A. ramosa* van den Bold, 1965, USNM 342104, 1 400 m off Newfoundland (from Benson *et al.* 1983, pl. 2 (fig. 1)). E. *A. caudata* van den Bold, 1965, HVH-7897, holotype, c. 1 000 m off Iceland (from Van den Bold 1965, pl. 1 (fig. 12)). Scale bar = 100 microns.

similar to the material available to us has been clarified by the re-illustration of Brady's (1880) 'Challenger' ostracods by Puri & Hulings (1976) (Table 4).

*Echinocythereis whatleyi* sp. nov.

Figs 35B-F, 36E-G, I-J

'*Xandarosina*' sp. Boomer, 1985: 64, fig. 7.

*Echinocythereis echinata* (non Sars, 1866) Benson *et al.*, 1983, pl. 2 (fig. 8).

*Derivation of name*

This species is named for Professor R. C. Whatley (University College of Wales, Aberystwyth) for his work on deep-water ostracod faunas.

TABLE 4

Previously-described species allocated to *Echinocythereis* and *Henryhowella* on the basis of the central muscle-scar pattern, following the revision of Puri & Hulings (1976).

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A Split anterior muscle scar

Genus *Echinocythereis*

*Cythere irpex* Brady, 1880

*Cythereis echinata* Sars, 1866

B Single, hooked anterior muscle scar

Genus *Henryhowella*

*Cythere circumdentata* Brady, 1880

*Cythere melobesioides* Brady, 1869

*Cythere ericea* Brady, 1880

*Cythere dasyderma* Brady, 1880

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*Holotype*

MF-0472, RV, TBD 3821, 1 525 m.

*Paratypes*

MF-0473, LV, TBD 6851, 2 916 m.

MF-0474, LV, TBD 3109, 900 m.

MF-0475, RV, TBD 3177, 1 000 m.

*Diagnosis*

Plump, blind species with broadly rounded AM and PM, and delicate surface ornamentation of small spines and lace-like reticulation.

*Description*

The species has a relatively delicate shell with broadly rounded AM and narrower rounded PM, more acuminate in RV. DM is short and straight, VM slightly concave. Antero-dorsal areas are somewhat compressed. Central valve area is plump, with the 'belly' of the lateral area just reaching to the VM. Highest point of the valve is over the ACA. No eyespots or ocular sinus. Valve surface is covered in fine spines arranged concentrically, being larger and more numerous postero-ventrally. Surface covered in a very fine, lace-like reticulation. AM has two, closely parallel rows of fine spines.

In internal view, marginal areas are narrow, with no vestibules. Hinge is weak, modified amphidont, with dorsally open terminal elements in LV. All elements appear smooth. MS consist of four elongate adductors, the second scar being the largest, with two small rounded anterior scars.



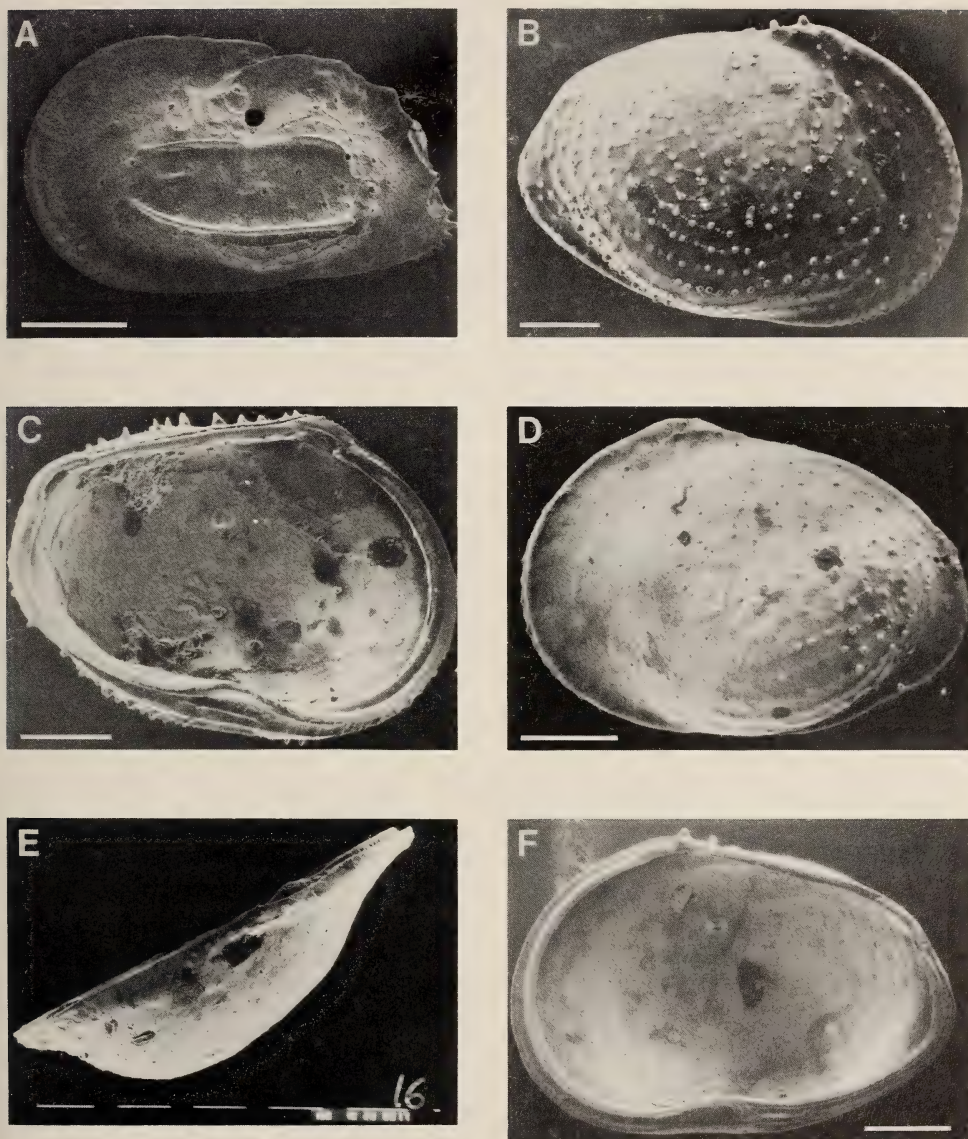


Fig. 35. A. *Ambocythere* sp. 3057, SAM-PQ-MF-0471, LV, TBD 3355, 2 070 m, SEM 3058. B-F. *Echinocythereis whatleyi* sp. nov. B. SAM-PQ-MF-0472, holotype, RV, TBD 3821, 1 525 m. C. SAM-PQ-MF-0473, LV internal view, TBD 6851, 2 916 m. D. SAM-PQ-MF-0474, LV, TBD 3109, 900 m. E. SAM-PQ-MF-0475, RV dorsal view, TBD 3177, 1 000 m. F. SAM-PQ-MF-0472, holotype, RV internal view, TBD 3821, 1 525 m. Scale bars = 100 microns.

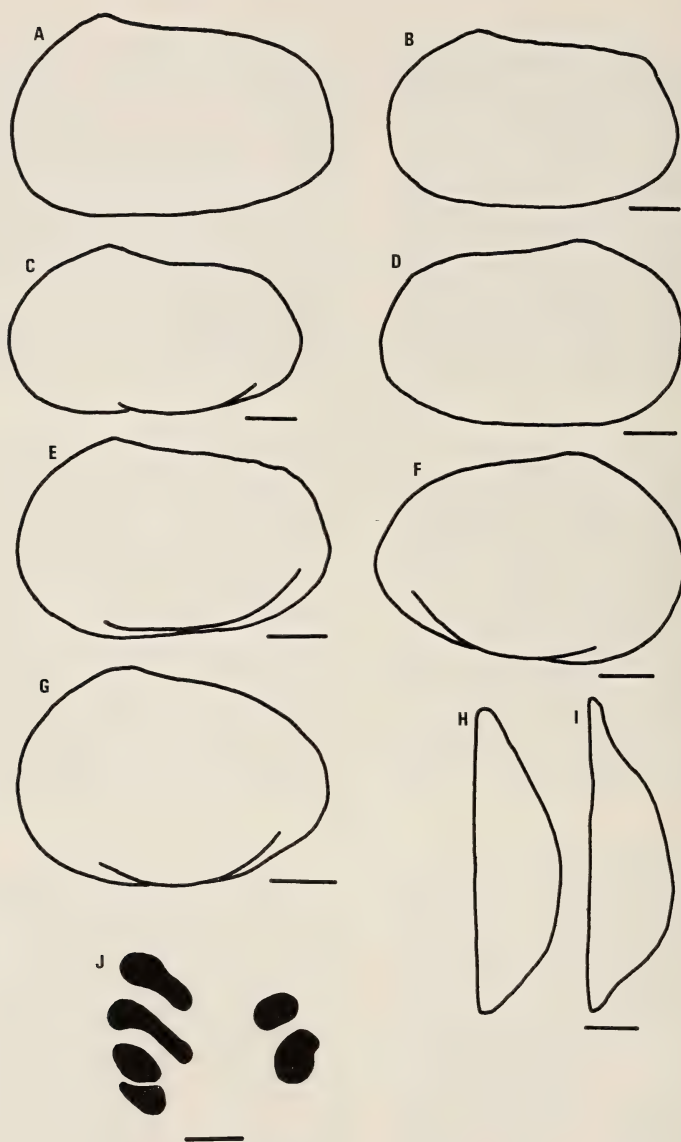


Fig. 36. Outlines of *Echinocythereis*. A, H. *E. echinata* (Sars, 1866). A. LV. H. Dorsal view. From Sars (1928, pl. 90). Localities unknown. B, D. *E. echinata* (Sars, 1866). B. DSDP site 611D-12 c.c. Pliocene. D. DSDP site 611D-1 c.c. Quaternary, NE Atlantic. From Whatley & Coles (1987, pl. 5 (figs 7-8)). C. *E. echinata* (Sars, 1866), specimen 13290, 2859, Quaternary, 2 859 m off NW Africa. From Rosenfeld & Bein (1978, pl. 1 (fig. 17)). E. *E. whatleyi* sp. nov. USNM 342109, station 77034-15, Quaternary, 3 000 m off Newfoundland. From Benson *et al.* (1983, pl. 2 (fig. 8)). F. *E. whatleyi* sp. nov. Holotype, SAM-PQ-MF-0472, TBD 3821, 1 525 m. G. *E. whatleyi* sp. nov., SAM-PQ-MF-0474, TBD 3109, 900 m. I. *E. whatleyi* sp. nov., SAM-PQ-MF-0475, TBD 3177, 1 000 m. J. *E. whatleyi* sp. nov., SAM-PQ-MF-0473, MS, LV, TBD 6851, 2 916 m. Scale bars: B-I = 100 microns; J = 30 microns; A, H = scales unknown.

*Dimensions (mm)*

	length	height
MF-0472	0,56	0,39
MF-0473	0,51	0,38
MF-0474	0,46	0,33

*Remarks*

*Echinocythereis whatleyi* sp. nov. is closely related to *Echinocythereis echinata* (Sars, 1866) and *E. irpex* (Brady, 1880). Sars (1928) considered *E. irpex* to be synonymous with *E. echinata*, and certainly these two species are more similar in lateral outline to each other than either is to *E. whatleyi*.

*Echinocythereis whatleyi* differs from both these species in having a plumper, less quadrate outline in lateral view. In particular, it has a shorter DM, with a less pronounced angle in the postero-dorsal region, and a more pronounced, rounded VM 'belly'. In addition, the degree of compression of the anterior marginal area in *E. whatleyi* is moderately strong in comparison to *E. echinata* (see dorsal views), and there is a difference in the shape of the postero-ventral and PM outlines, which are rounded and swept dorsally in *E. whatleyi* and 'obtusely blunted' in *E. echinata* (Sars 1928). Both *E. echinata* and *E. irpex* have a spinose ventro-lateral keel that is strongest posteriorly. This feature is lacking in *E. whatleyi* sp. nov.

Other species that have some similarities to *Echinocythereis whatleyi* are: *E. jacksonensis* (Howe & Pyeatt, 1935, in Howe & Chambers, 1935) from the Middle Eocene to Oligocene of south-eastern USA and the Caribbean (which is more elongate, and is sighted—see Howe & Howe 1973); *E. madremaestrae* van den Bold, 1988, from the Upper Miocene to Pliocene of the Caribbean (which has a very similar outline and ornamentation, but possesses a prominent eye tubercle); and a specimen referred to *E. irpex* (Brady) by Sylvester-Bradley & Benson (1971, fig. 24), which has two strong, short, antero-ventral ridges, and a denser overall covering of spines than our species.

Van den Bold (1966) described a new species of *Echinocythereis* from the Miocene of Gabon, but this taxon (*E. ecphyma*) has a hooked anterior MS, and consequently belongs to another genus.

*Echinocythereis echinata* (Sars) has been widely reported from the North Atlantic and the Mediterranean by numerous authors, in depths ranging from 60–600 m off Norway (Sars 1928: 195) to 4 700 m in the Central Atlantic (Tressler 1941). Whatley & Coles (1987) recorded it from Late Miocene to Quaternary sediments in the central North Atlantic. Rosenfeld & Bein (1978) recorded this species between 574 m and 2 859 m off north-western Africa.

Brady (1880) recovered *Echinocythereis irpex* from three sites in the central and South Atlantic, at depths between 900 m and 2 850 m.

We have recorded *E. whatleyi* over a latitudinal range of 19°S–36°S (Fig. 37) and a depth range of 730–2 916 m (Lower Neritic to Abyssal zones—Fig. 38). Most of our records lie within the Upper Bathyal Zone but the species



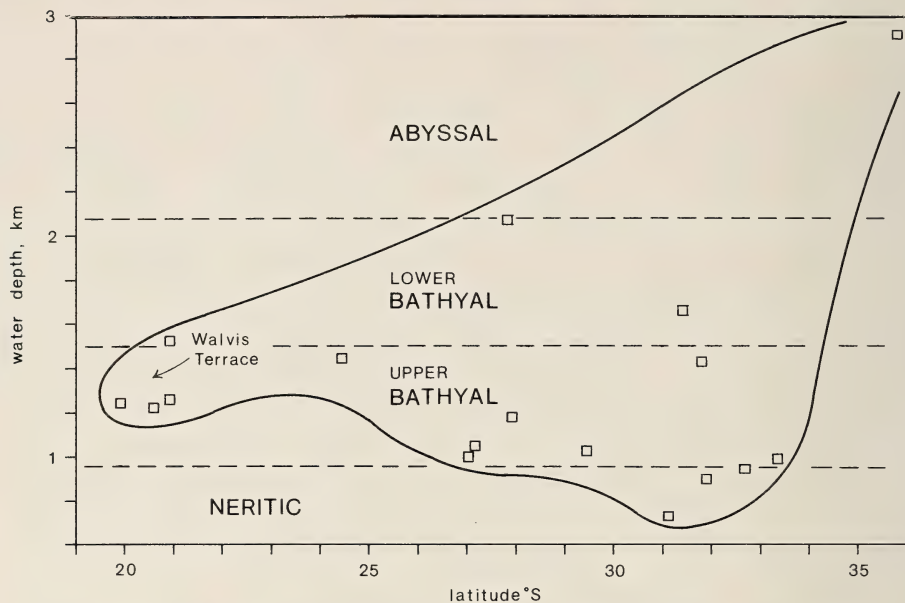


Fig. 37. Latitude and water depth of samples bearing *Echinocythereis whatleyi* sp. nov.

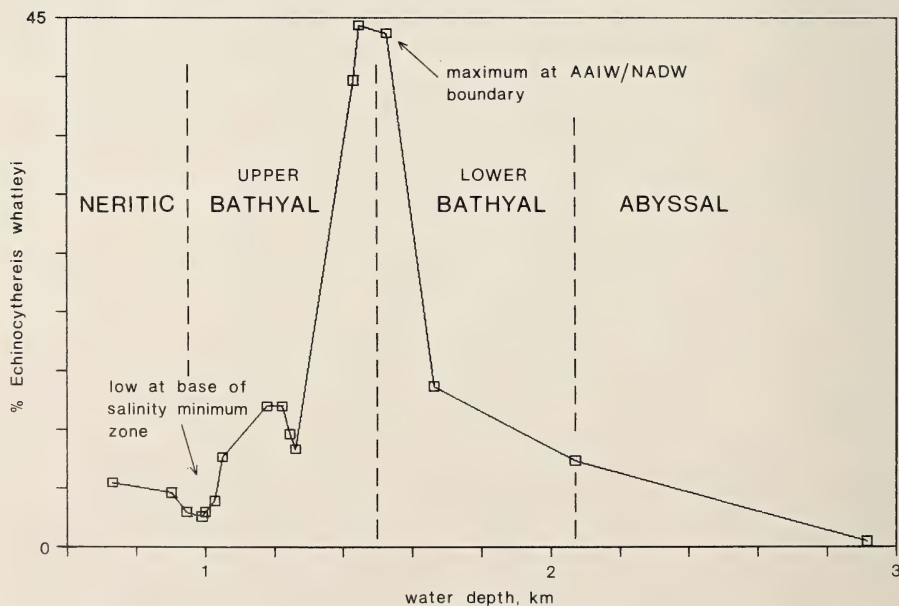


Fig. 38. *Echinocythereis whatleyi* sp. nov. as percentage of total ostracod fauna plotted against water depth. Values are three point running means.

is most abundant at the boundary of the AAIW and NADW masses (c. 1 500 m). There is an abundance low at the top of the Upper Bathyal Zone (i.e. immediately below the Salinity Minimum Zone of the AAIW mass), and the species decreases in abundance through the Lower Bathyal into the Abyssal zones. Benson *et al.* (1983) recorded the species (as *E. echinata*) between 2 800 m and 3 000 m off Newfoundland.

Off Walvis Bay, Peypouquet & Benson (1980) noted *Echinocythereis* between 974 m and 2 864 m, although they did not differentiate species. There are too few data points to make a detailed comparison with Figure 38, but their highest value does lie in the vicinity of 1 500 m. In contrast to our profile, however, the Walvis Bay data indicate a sharp rise in abundance in the vicinity of 3 km.

### Genus *Trachyleberis* Brady, 1898

#### *Trachyleberis* sp. 3017

##### Fig. 42A–B

?‘*Thalassocythere*’ sp. B Cronin, 1983, pl. 4 (figs B, E, G).

#### *Illustrated specimens*

MF–0476, RV, TBD 6851, 2 916 m.

MF–0477, LV, TBD 6851, 2 916 m.

#### *Remarks*

The type species of *Trachyleberis* Brady, 1898, is *Cythere scabrocuneata* Brady, 1880, and the holotype is lost. Puri & Hulings (1976, pl. 26 (figs 6, 8)) illustrated a topotype from the Inland Sea of Japan. Our species has less robust spines, no AM and PM rims, and lacks the antero-dorsal ocular ridge, and is not conspecific. In general aspect, however, it conforms with the genus.

Benson (e.g. Benson 1977, in Benson & Peypouquet 1983) seems to use the nomen nudum ‘*Thalassocythere*’ for deep-water *Trachyleberis*-like species and, judging from Benson (1977), when he lists (but does not illustrate) ‘*Thalassocythere*’ *acanthoderma* from the Miocene at DSDP sites 356 and 357, it is implied that *Cythere acanthoderma* Brady, 1880, is the comparative species for this group. An illustration of ‘*Thalassocythere*’ *acanthoderma* (Brady, 1880) from 3 000 m off Newfoundland (Benson *et al.* 1983, pl. 2 (fig. 9)), bears a close resemblance to Brady’s (1880, pl. 18 (figs 5a–e)) original illustrations, but differs from the lectotype of *Cythere acanthoderma* figured by Puri & Hulings (1976), which is probably a juvenile, in possessing a pointed PM outline; the lectotype has a rounded outline. Coles & Whatley (1989) have formalized the taxonomy of this group by erecting the genus *Legitimocythere*, with the type species *Cythere acanthoderma* Brady, 1880. Our species differs from *L. acanthoderma* (Brady, 1880) (as in Brady’s original illustrations) in lacking an AM rim,

in having a concave VM outline in lateral view, and having fewer and less massive and 'ragged' spines. It may be conspecific with ?'*Thalassocythere*' sp. B (Cronin, 1983), although our species has a less dense pattern of spines. R. C. Whatley (pers. comm. 1988) has suggested that our specimens are probably juveniles of *Legitimocythere acanthoderma* (Brady, 1880).

Rosenfeld & Bein (1978) did not record any trachyleberid-like species from off north-western Africa.

In the south-eastern Atlantic, *Trachyleberis* sp. 3017 is confined to the Abyssal Zone, where we have recorded it from two sites at 2 916 m and 4 736 m water depth. Here it constitutes 1 per cent and 33 per cent of the total ostracod fauna, respectively. Table 5 summarizes the geographical and depth ranges of the documented deep-sea species of *Trachyleberis*.

TABLE 5  
Distribution of deep-sea species of the genus *Trachyleberis* (including the nomen nudum '*Thalassocythere*\*').

Species	Reference	Age	Location	Depth (m)
<i>Trachyleberis acanthoderma</i>	Brady (1880)	Quaternary	Atlantic, Indian, Pacific	1 600–5 500
	Benson <i>et al.</i> (1983)	Quaternary	Newfoundland	2 600–3 210
	Ducasse & Pey-pouquet (1979)	Miocene–Quaternary	NE Atlantic (DSDP 403, 405)	?
	Whatley & Coles (1987)	Miocene–Quaternary	N Atlantic (DSDP 606–611)	2 445–3 884
<i>Trachyleberis</i> sp. 3017	this paper	Quaternary	SE Atlantic	2 916–4 736
<i>Trachyleberis</i> sp. B	Cronin (1983)	Quaternary	SE USA	341–739

\* '*Thalassocythere*' = *Legitimocythere* Coles & Whatley, 1989.

#### Genus *Henryhowella* Puri, 1957

*Henryhowella* has been widely reported in the literature from modern and Cenozoic deep-water sediments. The type species for *Henryhowella* is *Cythere evax* Ulrich & Bassler, 1904, and Puri's original diagnosis (1957 new name = *Howella* Puri, 1956), together with the type description of *Cythereis garretti* Howe & Mcguirt, 1935 (*in* Howe & graduate students 1935) (which is the type species for *Echinocythereis* Puri, 1954), distinguishes the genus *Henryhowella* from its close relative *Echinocythereis* on two criteria: 1. the possession of 'three well-developed longitudinal rows of spines in the posterior half of the carapace'; 2. having a single, hooked anterior MS (*Echinocythereis* has two small rounded anterior MS).



Conventional wisdom is to ascribe certain spinose taxa with a single hooked anterior MS to *Henryhowella*, irrespective of whether they possess a triplicate posterior ornamentation (e.g. Uffenorde 1981; Whatley & Coles 1987; Steineck *et al.* 1988). Those that do possess the latter feature are invariably placed in *Henryhowella asperrima* (Reuss, 1850) (e.g. Van den Bold 1960; Cronin 1983; Whatley & Coles 1987). This has the effect of modifying the generic concept and blurring its definition to the point of causing confusion with genera such as *Rocleberis* Bertels, 1969. It also reduces the only substantive distinguishing feature between *Echinocythereis* and *Henryhowella* to their different MS patterns. As a consequence, *Cythere evax* Ulrich & Bassler, 1904, should be considered a synonym of *Cypridina asperrima* Reuss, 1850 (e.g. Van den Bold 1957b, 1960), which becomes the type species of the genus *Henryhowella*. A problem here is that in his type description, Reuss (1850: 74), specifically stated that *Cypridina asperrima* has two posterior ridges and a median longitudinal furrow in the posterior part of the valve. Keij (1957) and Van den Bold (1960) have examined topotypes for Reuss's original material and both assumed that Reuss misidentified the valve architecture, although there has been no modern re-illustration of his topotypic material, nor the erection of a lectotype, if indeed the holotype is lost.

*Henryhowella melobesioides* (Brady, 1869)

Figs 42C–F, 43A–F, 44A–D, 47A

*Cythere melobesioides* Brady, 1869: 162, pl. 12 (figs 10–11); 1880: 108, pl. 18 (figs 1e–g). Puri & Hulings, 1976, pl. 25 (figs 1–2).

*Cythere nodulifera* Brady, 1869: 163, pl. 19 (figs 24–25).

*Henryhowella* sp. Keeler, 1981: 162–163, pl. 9 (fig. 14).

*Henryhowella* sp. Boomer, 1985: 25–27, pl. 1 (figs 6–8, 18).

non *Henryhowella* sp. Boomer, 1985: 25–27, pl. 3 (figs 38–39).

non *Cythere melobesioides* Brady, 1869. Brady, 1880, pl. 18 (figs 1a–d).

*Illustrated specimens*

MF-0478, RV, TBD 311, 184 m.

MF-0479, LV, TBD 311, 184 m.

MF-0480, LV, TBD 3561, 655 m.

MF-0481, RV, TBD 3561, 655 m.

MF-0482, LV, TBD 3704, 941 m.

MF-0483, RV, TBD 3704, 941 m.

MF-0484, RV, TBD 3383, 990 m.

MF-0485, RV, TBD 3383, 990 m.

MF-0486, LV, TBD 3383, 990 m.

MF-0487, LV, TBD 6851, 2 916 m.

MF-0488, LV, TBD 6851, 2 916 m.

MF-0489, LV, TBD 3383, 990 m.

*Remarks*

Accepting the current interpretation of non-plicate morphology, this species can be accommodated in the genus *Henryhowella*, and there are four species to which our material can be compared: *Henryhowella asperrima* (Reuss, 1850), *Henryhowella dasyderma* (Brady, 1880), *Henryhowella digitalis* Levinson, 1974 (in LeRoy & Levinson 1974), and *Henryhowella melobesioides* (Brady, 1869).

As discussed above, tri-plicate species (i.e. the 'typical' *Henryhowella* morphology) are generally automatically assumed to belong within *H. asperrima* (Reuss). This has led to the grouping of taxa whose synonymy appears doubtful but for which resolution requires redefinition of the types. To gauge the problem compare the following: Keij (1957, pl. 12 (figs 1–2)); Van den Bold (1960, pl. 4 (fig. 10)); Colalongo (1965, pl. 11 (figs 3–8)); LeRoy & Levinson (1974, pl. 12 (fig. 1)); Rosenfeld & Bein (1978, pl. 1 (fig. 23)); Cronin (1983, pl. 4 (fig. F)); Whatley & Coles (1987, pl. 5 (figs 9–11)). None of our material fits comfortably into the taxon currently interpreted as *Henryhowella asperrima*, even allowing for the range of morphological variation accepted by other authors. All the specimens that we have recovered have very weak or no lineation of spines in the posterior part of the valves; there are never three well-defined rows or ridges. The closest approximation to a tri-plicate morphology is shown in Figure 43C, but such are isolated examples in populations where there is gradation to the completely non-plicate state. As observed by Steinick *et al.* (1988) for their deep-sea Pacific populations, we feel unable to place specimens into a possibly polytaxonomic category.

Tertiary species referred to *H. asperrima* have been recorded from the vicinity of south-western Africa by Van den Bold (1966—Lower Miocene of Gabon) and Frewin (1987—Middle–Upper Eocene of the Agulhas Bank). Dingle (1976) recorded a form very close to Frewin's species as *Henryhowella* sp. This ranges from Lower Eocene to Upper Oligocene in the J(c)–1 borehole on the continental shelf off Natal (south-eastern Africa), and is probably the same species as a worn specimen referred to Indet. sp. 2314 from Upper Cenomanian strata in the same borehole (Dingle 1985). The latter record was possibly a downhole contaminant from overlying Tertiary strata. These local records are all probably of the same species (whether or not they can ultimately be referred to Reuss's species is an open question), which seems to have a range Lower Eocene to Miocene.

*Henryhowella digitalis* Levinson, 1974 (in LeRoy & Levinson 1974), was erected as a variety of *H. asperrima* to accommodate specimens with a reticulate/spinose ornamentation. LeRoy & Levinson (1974) speculated that this was a 'deep-water variant' of *H. asperrima*. Some of our specimens do show a degree of reticulation, but it is not a consistently developed feature.

*Henryhowella dasyderma* (Brady, 1880) is a non-plicate species. Brady (1880) included several morphotypes in his original description, one of which (1880, pl. 17 (fig. 4e–f)) has a sharp ventro-lateral ridge. The lectotype designated by Puri & Hulings (1976, pl. 11 (figs 10–11)) from 'Challenger' site 296

(south-eastern Pacific) is very similar to our material, but we have not assigned our specimens to it, because Brady himself (1880) believed that the populations that he recovered from off the south-western Cape were closer to *Cythere melobesioides* Brady, 1869. However, he did remark (1880: 105) that *Cythere dasyderma* was a deep-water taxon that occurs world-wide. It has been subsequently recorded by Rosenfeld & Bein (1978) from 1 029–2 480 m off north-western Africa, and Whatley & Coles (1987) from early Pliocene to Quaternary of the North Atlantic.

*Henryhowella melobesioides* (Brady, 1869) was recorded by Brady (1880) from 'Challenger' site 142 off the Cape Peninsula in 150 fm (274 m) water depth. The type species was from Mauritius and Brady (1880) also identified it from Australia, but these (pl. 18 (fig. 1a–d)) appear not to be conspecific. Our material is conspecific with the specimen illustrated by Puri & Hulings (1976, pl. 25 (figs 1–2)), but there is some variation in ornamentation within the population, particularly in the prominence of a weak ridge that lies almost parallel to the postero-ventral margin, a feature noted in the illustration in Brady (1880, pl. 18 (fig. 1g)). The lateral surface spines are arranged concentrically in the anterior part of the valve, and randomly or with a weak elongation that tends to converge into a chevron with its apex towards the PM. No consistent morphological variations are observed between specimens from different depths, although individuals from shallower water tend to have the more nodose spines described by Brady (1880). MS patterns are identical when observed over a range 655–2 916 m (no good views were obtained from shallow-water examples). It is possible that we have more than one species in our populations but, until the uncertainty of the taxonomic position of forms currently referred to *H. asperrima* (Reuss) and their relationship to *H. dasyderma* (Brady) have been clarified, there seems little point in attempting to subdivide the various morphotypes of our *H. melobesioides* (Brady) population.

Off south-western Africa, *Henryhowella melobesioides* (Brady, 1869) has been found over a latitudinal range 19°S–36°S (Fig. 39), and a depth range of 100–2 916 m (Fig. 40). In the Neritic Zone, it is confined to water greater than 600 m north of 29°S, where we suspect it cannot survive in either low oxygenated water (associated with the upwelling cells north of 25°S) or influxes of less saline and/or suspensate-rich water from the Orange River on the continental shelf between 25°S and 29°S. The upwelling cells on the shelf south of 29°S do not sustain sufficiently high productivity in the water column to result in low oxygen layers.

Figure 40 shows that on the continental shelf (i.e. less than 300 m), *H. melobesioides* is a minor element in the ostracod population (generally <10%). Its abundance steadily increases with water depth, so that overall within the Neritic Zone it constitutes a mean of 31 per cent (range 0,1–100%). In the Upper Bathyal Zone it is the dominant ostracod taxon, generally forming more than 60 per cent of the total population (mean of 73%, range 19–100%) but, between about 800 m and 1 000 m, which includes the Neritic/Bathyal



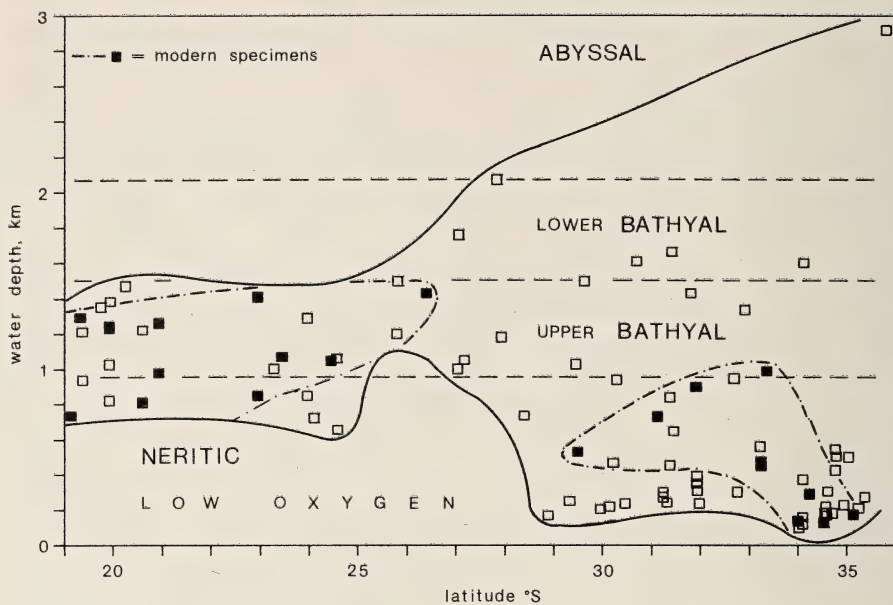


Fig. 39. Latitude and water depth of samples bearing *Henryhowella melobesioides* (Brady, 1869). Note the absence of this species from the low  $O_2$ , and low salinity/high suspensate continental shelves off Walvis Bay/Lüderitz, and Orange River, respectively.

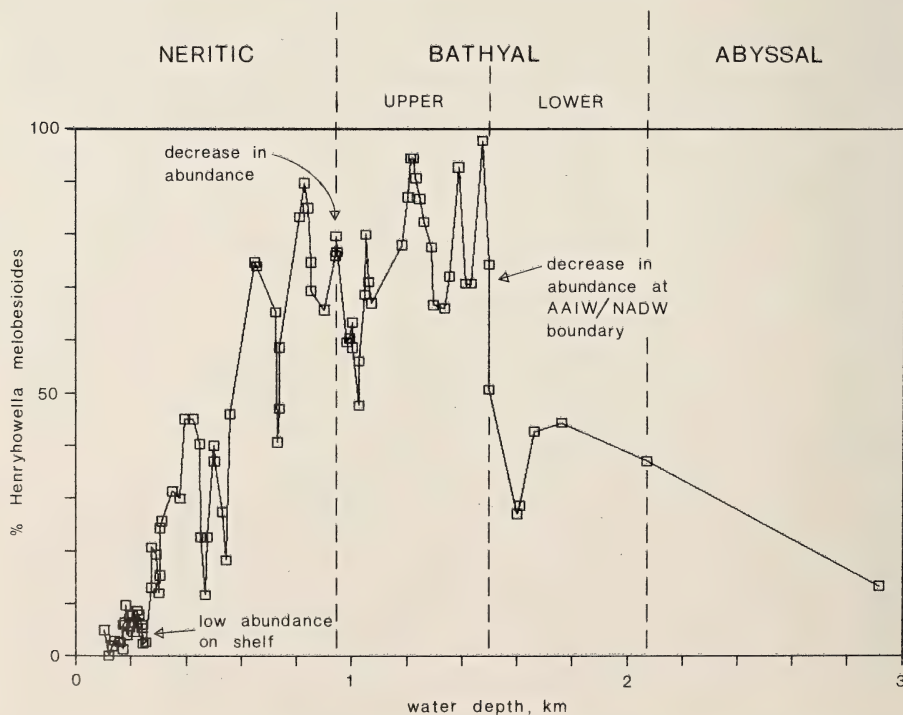


Fig. 40. *Henryhowella melobesioides* (Brady, 1869) as percentage of total ostracod fauna plotted against water depth. Values are three point running means.

boundary, there are large fluctuations in its abundance. Similarly, on approaching the Upper/Lower Bathyal Zone boundary (i.e. the shear zone between the AAIW and NADW masses), there is a large fall in abundance, that continues through the Lower Bathyal Zone (mean 39%, range 28–71%) into the Abyssal Zone (mean 20%, range 6–34%). Clearly, this species has a wide tolerance of temperature and salinity, but it is relatively less successful in unstable, or mixed zones. In this respect it shows a distribution pattern that is the reverse of *Buntonia rosenfeldi* sp. nov.

Modern specimens were identified on two criteria: shell transparency and good preservation of spines. They were encountered in two distinct areas. North of 26°S the entire distribution zone contains modern valves (i.e. in both the Lower Neritic and Upper Bathyal Zones), whereas farther south the modern population is confined between 29°S and 35°S and almost solely to the Neritic Zone (Fig. 39).

Peypouquet & Benson (1980) recorded *Henryhowella* from their traverse off Walvis Bay. There are too few data points to make a meaningful comparison with our results, but a plot of the abundance of *Henryhowella* (Fig. 41) indicates similar trends to Figure 40. We do not know if the species they recorded was *H. melobesioides* but suspect so, because the latitudinal ranges of the data sets overlap.

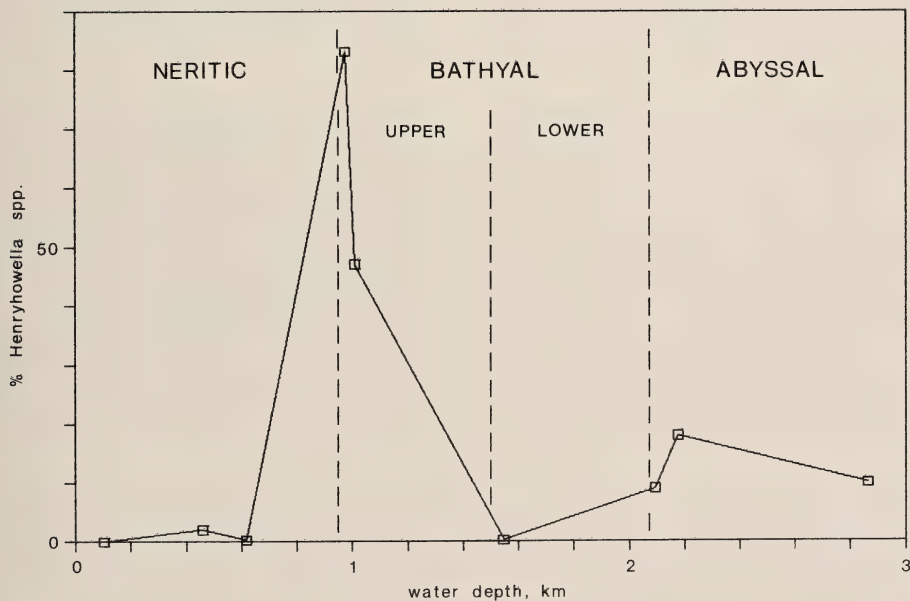


Fig. 41. *Henryhowella* species as percentage of total ostracod fauna plotted against water depth for a profile off Walvis Bay. Data computed from Peypouquet & Benson (1980).

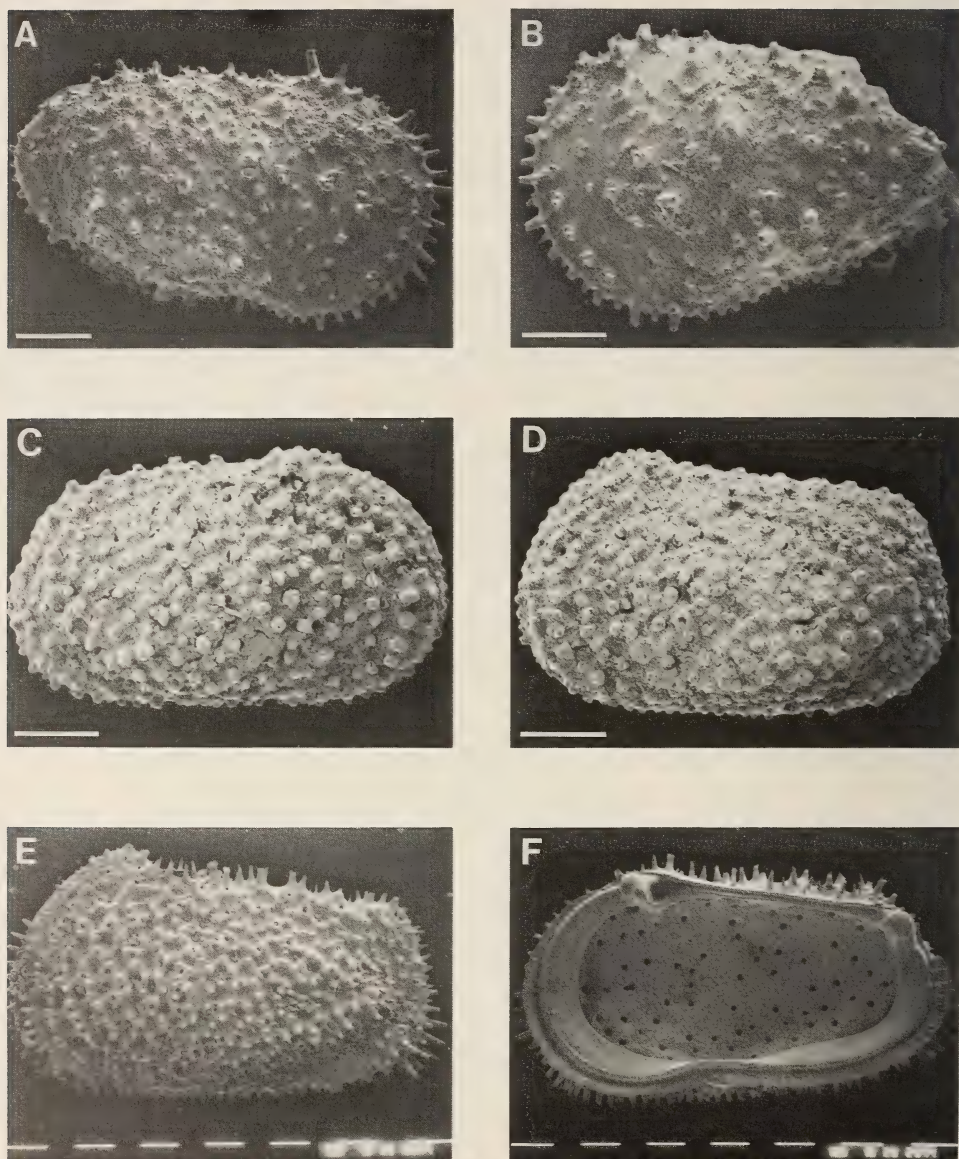


Fig. 42. A-B. *Trachyleberis* sp. 3017, TBD 6851, 2 916 m. A. SAM-PQ-MF-0476, RV, SEM 3017. B. SAM-PQ-MF-0477, LV, SEM 3024. C-F. *Henryhowella melobesioides* (Brady, 1869). C. SAM-PQ-MF-0478, RV, TBD 311, 184 m, SEM 2625. D. SAM-PQ-MF-0479, LV, TBD 311, 184 m, SEM 2626. E. SAM-PQ-MF-0480, LV, TBD 3561, 655 m, SEM 2591. F. SAM-PQ-MF-0481, RV internal view, TBD 3561, 655 m, SEM 2594.

Scale bars = 100 microns.



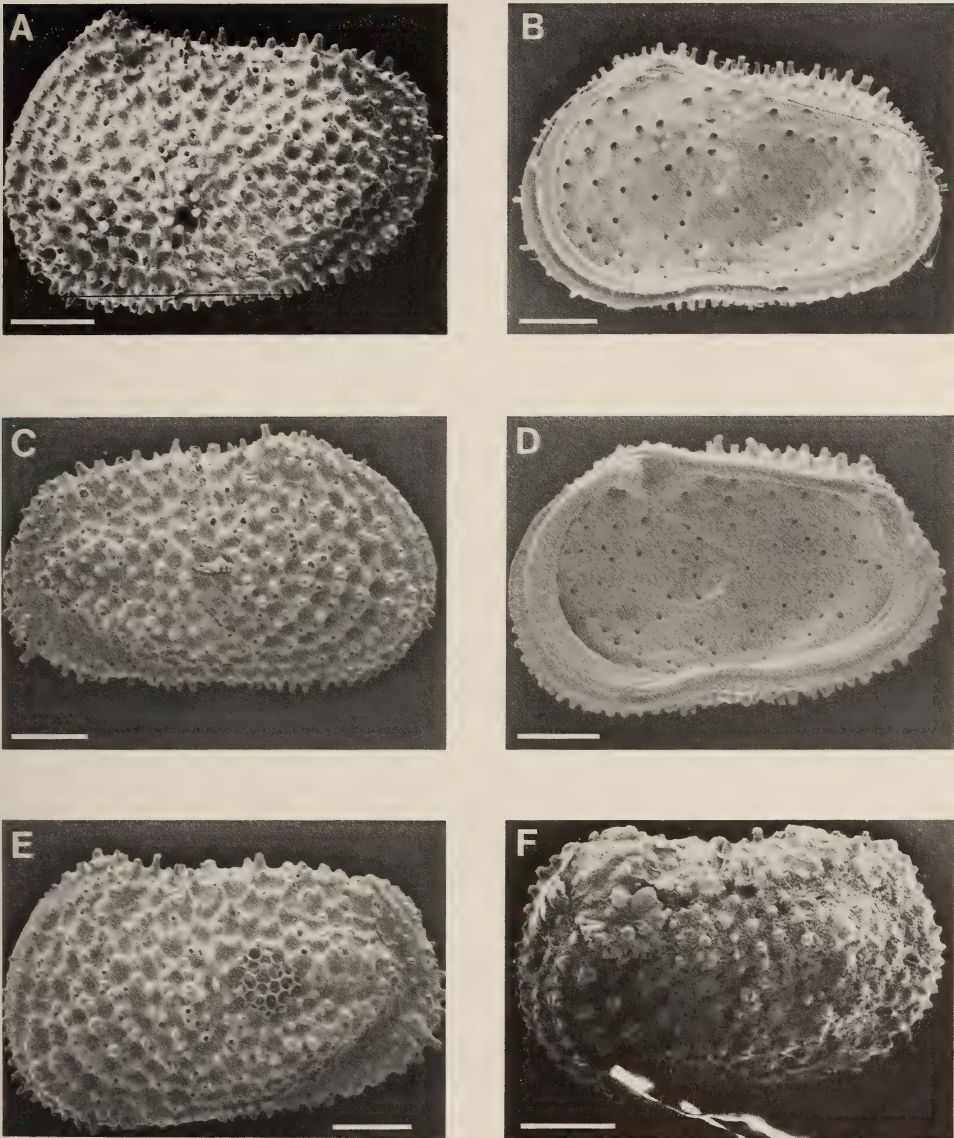


Fig. 43. A-F. *Henryhowella melobesioides* (Brady, 1869). A. SAM-PQ-MF-0482, LV, TBD 3704, 941 m, SEM 2630. B. SAM-PQ-MF-0483, RV internal view, TBD 3704, 941 m, SEM 2632. C. SAM-PQ-MF-0484, RV, TBD 3383, 990 m, SEM 2552. D. SAM-PQ-MF-0485, RV internal view, TBD 3383, 990 m, SEM 2561. E. SAM-PQ-MF-0486, LV, TBD 3383, 990 m, SEM 2551. F. SAM-PQ-MF-0487, LV, TBD 6851, 2 916 m, SEM 2636. Scale bars = 100 microns.



Fig. 44. MS of *Henryhowella melobesioides* (Brady, 1869). A. SAM-PQ-MF-0481, RV, TBD 3851, 655 m, SEM 2621. B. SAM-PQ-MF-0483, RV, TBD 3704, 941 m, SEM 2634. C. SAM-PQ-MF-0489, LV, TBD 3383, 990 m, SEM 2556. D. SAM-PQ-MF-0488, LV, TBD 6851, 2 916 m, SEM 2639. Open dots are normal pores. Scale bars are 100 microns.

#### Subfamily Pennyellinae Neale, 1975

Neale (1975) established this taxonomic category to accommodate certain blind, reticulate trachyleberids, and identified three genera that belonged here: *Pennyella* Neale, 1974, Santonian (Western Australia—Neale 1974) to Maastrichtian (north-western Pacific—Swain 1973); *Agulhasina* Dingle, 1971, Maastrichtian (southern Africa); *Agrenocythere* Benson, 1972, Eocene (Atlantic) to Recent (pandemic). We now add a fourth: *Rugocythereis* gen. nov., Miocene to Quaternary (pandemic—Brady 1880; Whatley & Coles 1987).

#### *Rugocythereis* gen. nov.

##### *Derivation of name*

Latin *rugosa*—rough, reference to coarse texture of surface ornamentation.

##### *Type species*

'*Oxycythereis*' *horridus* Whatley & Coles, 1987.

##### *Diagnosis*

Blind, elongate-sub-quadrate trachyleberid with coarsely reticulate and/or stout spinose ornamentation. Strongly sexually dimorphic with males significantly more elongate than females. Females typically possess an antero-dorsal marginal frill. Valves are inflated postero-ventrally and compressed in the AM

areas, with strong AM and PM rims. Typically there is a prominent cleft between the PM rim and the area of postero-ventral inflation. Hinge is modified amphidont, with weak ATE in RV.

#### Remarks

*Rugocythereis* gen. nov. is a pandemic genus that includes several taxa previously placed in the nomen nudum '*Oxycythereis*' Benson, 1974. It is closest to *Pennyella* Neale, 1974, but the two genera differ on the following features:

1. *Rugocythereis* lacks the prominent vertical postero-dorsal ridge.
2. *Rugocythereis* lacks the prominent ventro-lateral ridge that terminates in a posterior elevation.
3. *Pennyella* has a more triangular-shaped PM outline, with a distinctive postero-dorsal concavity.
4. Females of *Rugocythereis* have a distinctive antero-dorsal marginal frill.
5. The hinges are somewhat different: *Pennyella* has a peg-like ATE in the RV, with a post-adjacent rounded socket, whereas in *Rugocythereis* the RV ATE is low and elongate, has a narrow groove on its dorsal side, and has no post-adjacent rounded socket.

The two genera have very similar MS patterns, which include a ventrally deflected second adductor and two very close, almost fused, third and fourth adductors.

*Rugocythereis* gen. nov. is a deep-water genus, for which four species have been formally described: *R. horridus* (Whatley & Coles, 1987), *R. dorsoserrata* (Brady, 1880, emend. Puri & Hulings, 1976), and two species originally placed in *Pennyella* (*P. fortetdimorphica* Coles & Whatley, 1989, and *P. praedorsoserrata* Coles and Whatley, 1989). In addition, Whatley & Coles (1987) recorded two possible species in open nomenclature ('*Oxycythereis*' sp. 1 and '*Oxycythereis*' sp. 2). Several other modern and fossil species of *Rugocythereis* may be included in the nomen nudum '*Oxycythereis*' (see Kempf 1986a, 1986b), but their status is uncertain. This is because the references have lacked either illustrations or descriptions or both, which introduces confusion over the comparability of *R. dorsoserrata* (Brady, 1880) and the validity of additional specific taxa (e.g. Benson 1977; Peypouquet & Benson 1980; Benson *et al.* 1983).

Table 6 lists known and possible taxa that belong in *Rugocythereis* gen. nov. Given the limitations of the uncertain taxa, the genus may have an age range of Eocene to Recent and a water depth range for modern species of 730–3 526 m.

Guernet (1985, pl. 4 (fig. 9)) described a species under *Wichmanella*? cf. *W.?* *reticulata*, which has a similar valve outline and ornamentation to *R. horridus*. This taxon was recorded in Lower Eocene strata at DSDP site 245 in the south-western Indian Ocean.

No species referable to *Rugocythereis* (including the nomen nudum taxa '*Oxycythereis*') was reported from Quaternary deep-water sites off the south-eastern USA (Cronin 1983) or north-western Africa (Rosenfeld & Bein 1978).



TABLE 6  
Geographical and water depth distribution of species of *Rugocythereis* gen. nov.

Species	Reference	Age	Location	Quaternary depth (m)
<i>Rugocythereis dorso-serrata</i> (Brady, 1880)	Brady (1880)	Quaternary	S Atlantic	2 850
<i>Rugocythereis horridus</i>	Whatley & Coles (1987)	Miocene–Quaternary	N Atlantic	2 445–3 526
		Pliocene–Quaternary	SW Pacific	
	Ducasse & Pey-pouquet (1979) this paper	Miocene Quaternary	SW Indian NE Atlantic (DSDP 405)	3 000
		Quaternary	SE Atlantic	730–2 916
<i>Rugocythereis?</i> spp.	Benson (1974)	Eocene–Pliocene	W Indian (DSDP 237, 238)	?
	Benson <i>et al.</i> (1983)	Quaternary	NW Atlantic	3 210
	Benson (1977)	Eocene–Pleistocene	S Atlantic (DSDP 356, 357)	?
	Peypouquet & Benson (1980)	Quaternary	SE Atlantic	2 094–2 644
<i>Rugocythereis</i> sp. 1	Whatley & Coles (1987)	Miocene	N Atlantic	
<i>Rugocythereis</i> sp. 2	Whatley & Coles (1987)	Pliocene	N Atlantic	

*Rugocythereis horridus* (Whatley & Coles, 1987)

Figs 47B–F, 48

'*Oxycythereis*' *horridus* Whatley & Coles, 1987: 76–78, pl. 5 (figs 18–22).

*Henryhowella* sp. Boomer, 1985: 25–27, pl. 3 (figs 38–39).

non *Henryhowella* sp. Boomer, 1985: 25–27, pl. 1 (figs 6–8).

*Illustrated specimens*

MF-0490, RV, TBD 2677, 1 662 m.

MF-0491, LV, TBD 6851, 2 916 m.

MF-0492, RV, TBD 6851, 2 916 m.

MF-0493, RV, TBD 6851, 2 916 m.

*Remarks*

*Rugocythereis horridus* (Whatley & Coles) was originally described from Miocene to Quaternary strata at DSDP sites from Leg 94 in the north central Atlantic, and was also recorded from Pliocene to Quaternary in the south-

western Pacific, and Miocene from the Indian Ocean (Whatley & Coles 1987). We record it in the south-eastern Atlantic between 29°S and 36°S, in water depths of 730–2 916 m (Fig. 45). The species was found in only 16 per cent of the bathyal and abyssal sites, and Figure 46 shows that *R. horridus* ranges from lower neritic to abyssal depths and that it is most abundant in the Upper Bathyal Zone. In the lower part of the Neritic Zone, abundances are low (mean: 4% total ostracod fauna, range nil), but in the Bathyal Zone the species is relatively abundant (mean: 24%, range 4–100%). There appears to be a decrease in abundance with increasing depth through the Bathyal Zone, and the single site in the Abyssal Zone (2 916 m) has the lowest abundance of our data set (2%).

The species recorded by Ducasse & Peypouquet (1979) as '*Oxycythereis dorsoserrata* [sic] from DSDP site 405 in the Rockall Basin (north-eastern Atlantic) probably belongs in *R. horridus*.

*Rugocythereis horridus* is closely related to *R. dorsoserrata* (Brady, 1880), which has been re-illustrated by Puri & Hulings (1976), who selected a lectotype from Brady's original 'Challenger' material. Positive identifications of *Rugocythereis dorsoserrata* (Brady, 1880) have been: Brady's original record from 2 605 m (1 425 fm) north of Tristan da Cunha in the South Atlantic; Whatley & Coles's (1987) record from Miocene–Quaternary strata from DSDP Leg 94 sites in the North Atlantic; and two specimens identified as *Cythere suhmi* Brady, 1880, by Ducasse & Peypouquet (1979, pl. 2 (figs 5–6)) from the late Pliocene

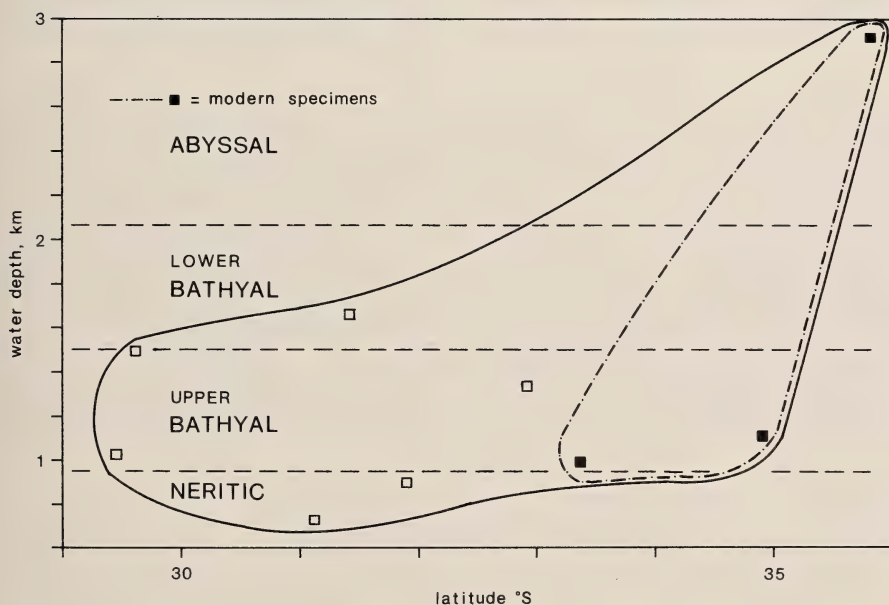


Fig. 45. Latitude and water depth of samples bearing *Rugocythereis horridus* (Whatley & Coles, 1987).

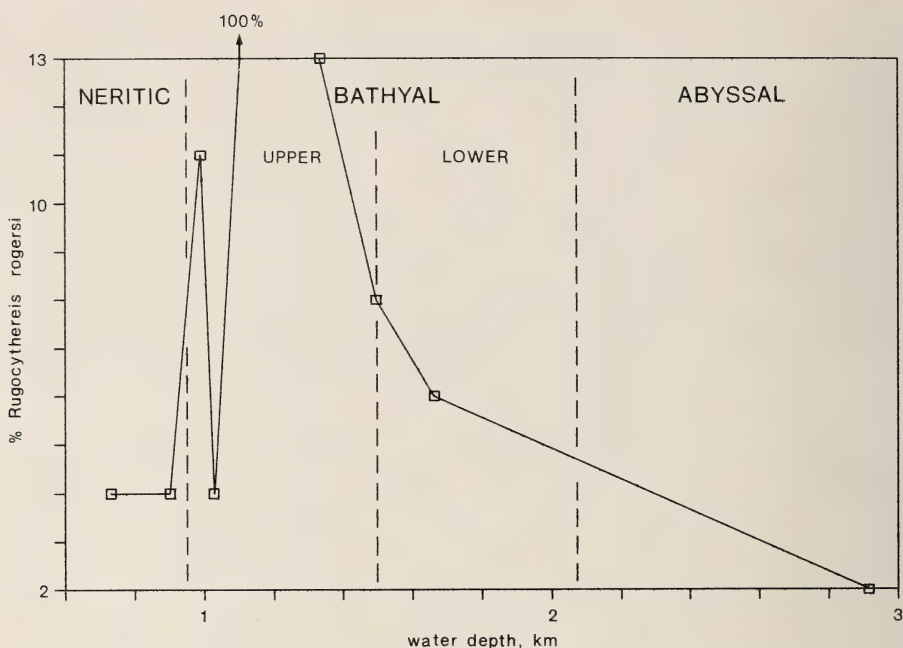


Fig. 46. *Rugocythereis horridus* (Whatley & Coles, 1987) as percentage of total ostracod fauna plotted against water depth. Values have not been smoothed.

of DSDP site 403 on Hatton Bank (north-eastern Atlantic), which are probably conspecific. These records suggest an age range Miocene to Quaternary for *R. dorsoserrata*.

Benson *et al.* (1983) recorded '*Oxycythereis*' *dorsoserrata* (Brady, 1880) (which they equated with '*O.*' *dorsoserrata* of Ducasse & Peypouqueti 1979) from a sample at 3 210 m off Newfoundland, but did not illustrate the specimen.

Peypouquet & Benson (1980) recorded '*Oxycythereis*' from their traverses in the Cape and Angola basins. These may refer to species of *Rugocythereis*, although there were no accompanying illustrations. The data are too sparse to plot, but abundances at the three sites were: Walvis transect—2 094 m, 0.2 per cent; 2 117 m, 1 per cent; Angola Basin—2 644 m, 0.7 per cent. These are lower values than we have determined for similar depths, but indicate that the taxon is rare.

Subfamily Bradleyinae Benson, 1972

Genus *Poseidonamicus* Benson, 1972

Whatley *et al.* (1983) have expressed reservations about the suprageneric placement of *Poseidonamicus*, but we will follow Benson's original classification for the present.



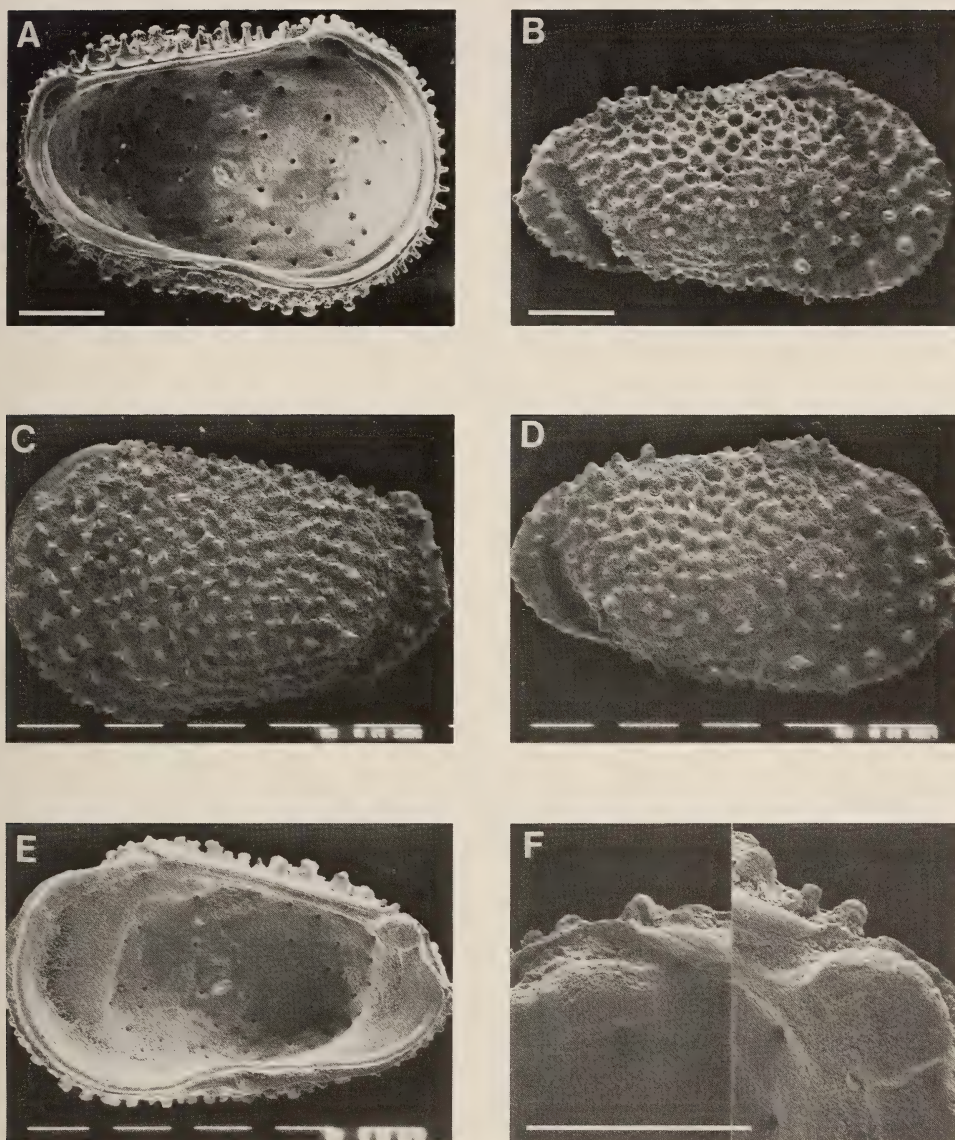


Fig. 47. A. *Henryhowella melobesioides* (Brady, 1869), SAM-PQ-MF-0488, LV internal view, TBD 6851, 2 916 m, SEM 2638. B-F. *Rugocythereis horridus* (Whatley & Coles, 1987). B. SAM-PQ-MF-0490, RV, TBD 2677, 1 662 m, SEM 3030. C-F. TBD 6851, 2 916 m. C. SAM-PQ-MF-0491, LV, SEM 3008. D. SAM-PQ-MF-0492, RV, SEM 3009. E. SAM-PQ-MF-0493, RV internal view, SEM 3012. F. SAM-PQ-MF-0493, RV ATE and PTE, SEM 3013 and 3014. Scale bars = 100 microns.

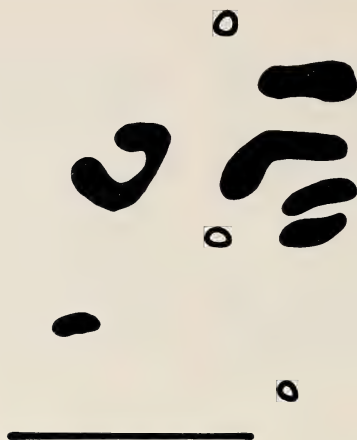


Fig. 48. MS of *Rugocythereis horridus* (Whatley & Coles, 1987). SAM-PQ-MF-0493, RV, TBD 6851, 2 916 m, SEM 3015. Open dots are normal pores. Scale bar = 100 microns.

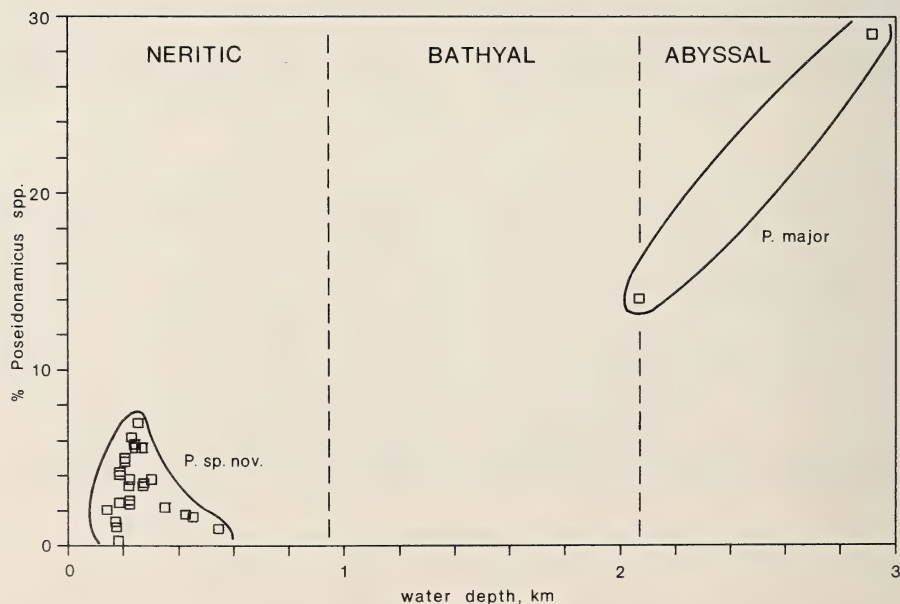


Fig. 49. Latitude and water depth of samples bearing *Poseidonamicus* species. The populations of *P. major* Benson, 1972 (deep-water species), and *P. panopsus* Whatley & Dingle, 1989 (shallow-water species) are outlined. They are separated by 1 500 m of the water column, which contains several effective physico-chemical barriers.

Whatley (1985) discussed the colonization of bathyal and abyssal environments by species of *Poseidonamicus*, and he concluded that since early Palaeogene time the genus has been confined to water depths greater than 1 000 m. However, recent work on the ostracod fauna offshore south-western Africa has located two species of the genus, one of which is blind and lives at abyssal depths (*P. major* Benson, 1972), and one of which is sighted and lives on the outer continental shelf/upper slope (*P. panopsus* Whatley & Dingle, 1989). Figure 49 shows the distribution and abundances of these two species in the south-eastern Cape Basin. It is significant that the habitats of the two species, which are both extant, are separated by 1 500 m of water that includes the Salinity Minimum Zone of the AAIW and the boundary between the AAIW and NADW water masses. These must be very effective barriers in maintaining the identity of the two species.

*Poseidonamicus major* Benson, 1972

Figs 50A–F, 51A–B

*Poseidonamicus major* Benson, 1972: 52–53, pl. 8 (fig. 5), pl. 10 (figs 1–6), text-figs 20, 22.

*Illustrated specimens*

MF–0494, RV, TBD 6851, 2 916 m.

MF–0495, LV, TBD 6851, 2 916 m.

MF–0496, LV, TBD 6851, 2 916 m.

MF–0497, RV, TBD 6851, 2 916 m.

*Remarks*

Our material is identical to the holotype (USNM 174335), except for its MS pattern, which in the Cape Basin specimens show an indented ventral scar in the anterior pair, and two 'dog's bone'-shaped central scars in the adductors.

*Poseidonamicus major* differs from the shelf/upper slope species of the genus that has recently been discovered living in neritic depths (120–545 m) off south-western Africa (*P. panopsus* Whatley & Dingle, 1989) in several respects. The new species has a prominent eye tubercle, is generally more quadrate in lateral outline, and lacks the strong, curved anterior dorso-lateral ridge that is a characteristic feature of *P. major*. Their MS are very similar, although in *P. panopsus* the lower anterior scar is more V-shaped than in our specimens of *P. major*.

Frewin (1987) recorded an Eocene species from the Agulhas Bank as ?*Poseidonamicus* sp. A126. This is a sighted form that has some architectural features similar to the type species of *Poseidonamicus*, but whose overall morphology suggests that it belongs to an undescribed taxon.

The holotype of *Poseidonamicus major* is from the Mozambique Channel (south-west of Europa Island) at a depth of 2 995 m, where Benson (1972) recorded a bottom water temperature of 1.6°C. Off south-western Africa, we



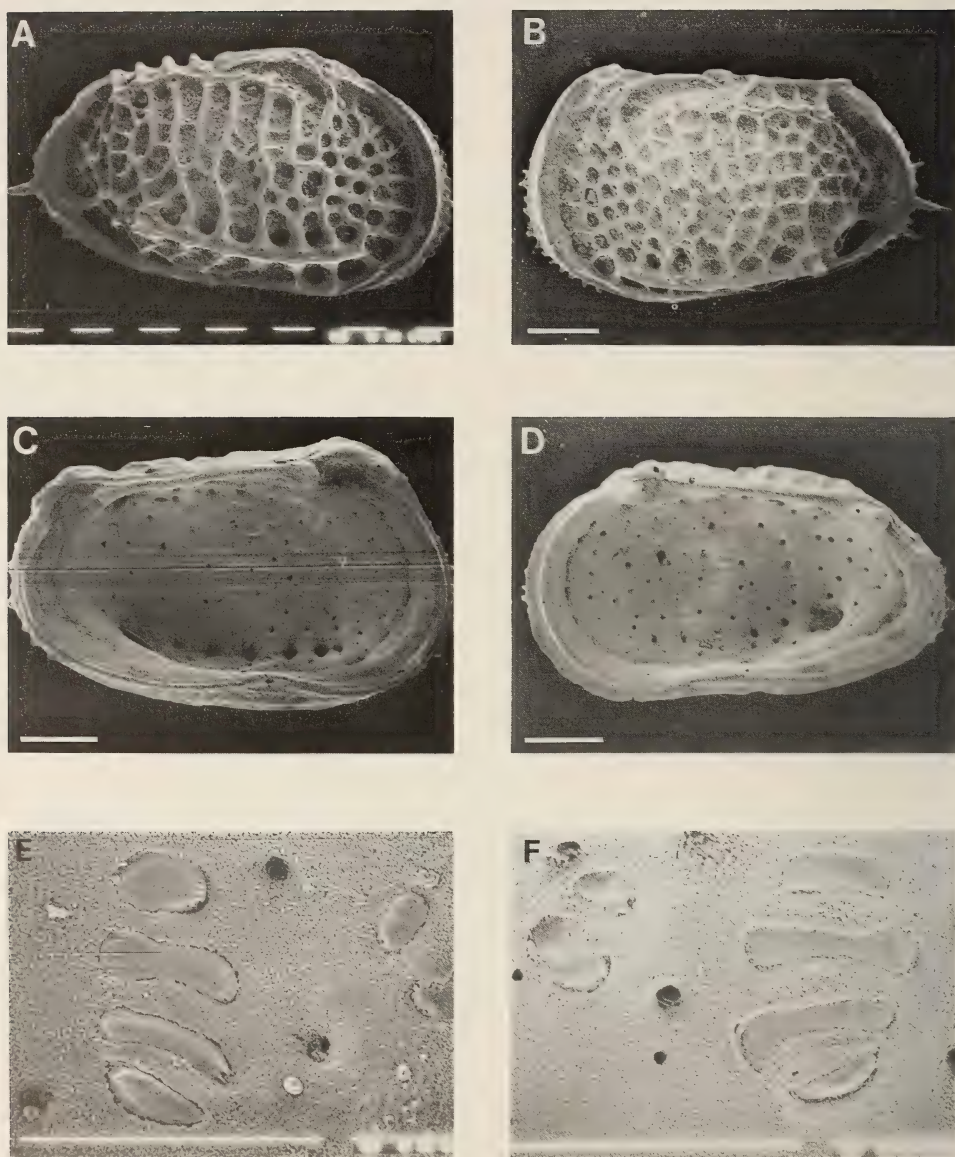


Fig. 50. A-F. *Poseidonamicus major* Benson, 1972, TBD 6851, 2 916 m. A. SAM-PQ-MF-0494, RV, SEM 2929. B. SAM-PQ-MF-0495, LV, SEM 2926. C. SAM-PQ-MF-0496, LV internal view, SEM 2931. D. SAM-PC-MF-0497, RV internal view, SEM 2933. E. SAM-PQ-MF-0496, LV MS, SEM 2932. F. SAM-PQ-MF-0497, RV MS, SEM 2935. Scale bars = 100 microns.

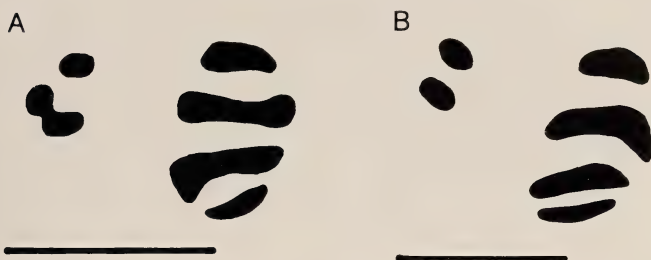


Fig. 51. MS of *Poseidonamicus major* Benson, 1972. A. SAM-PQ-MF-0497, RV, TBD 6851, 2 916 m, SEM 2935. B. USNM 174354, RV, IIOE 363B, 2 995 m, Mozambique Channel (from Benson 1972, fig. 22B). Scale bars = 100 microns.

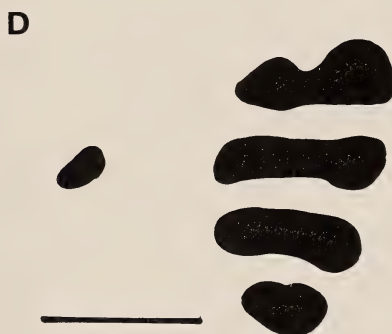
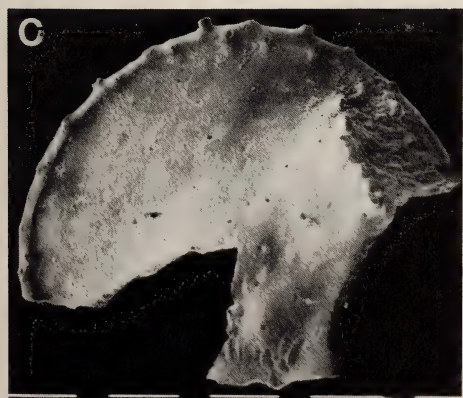


Fig. 52. A-B, D. Indet. sp. 62, TBD 3870, 1 026 m. A. SAM-PQ-MF-0498, LV. B, D. SAM-PQ-MF-0499, RV. B. Internal view. D. MS. C. Indet. sp. 23, SAM-PQ-MF-0500, TBD 3174, 1 050 m. Scale bars: A-C = 100 microns; D = 30 microns.



found the species at two sites within the Abyssal Zone: TBD 3355 (2 070 m) and TBD 6851 (2 916 m) (Fig. 49). In the former, which lies at the top of the Abyssal Zone, *P. major* accounts for 14 per cent of the total ostracod fauna and is the third most abundant taxon, but all the specimens were relict. At TBD 6851 (2 916 m), this species is the second most abundant taxon (29%), 6 per cent of which were modern specimens (1,7% of total ostracods).

In his original discussion of *Poseidonamicus*, Benson (1972) erected four new species, all of which are extant: *P. major*, *P. minor*, *P. nudus*, and *P. pinto*. He did not quote depth ranges for individual species, but reference to his table 2 shows the ranges that he recorded for the modern genus in various oceans, as follows: Atlantic 1 227–5 020 m; Indian 1 190–3 995 m; and Pacific 2 089–3 292 m. Whatley (1985) has discussed the evolutionary history of the genus and concluded that it originated in the south-western Pacific, probably in the Palaeocene, from a species such as *Hermanites sagitta* Bate, 1972, which had a continental-shelf habitat. During a phase of rapid mutation in the early Tertiary, the earliest forms of *Poseidonamicus* migrated into bathyal and later (in the Miocene) into abyssal habitats. Whatley (1985) did not have sufficient data to postulate the evolution of *P. major*, which is morphologically distinct from the other Tertiary forms. He recorded it in the Miocene of the south-western Pacific, but Benson (1972: 53) stated that it occurs in the Oligocene of DSDP site 117 (north-eastern Atlantic). Benson & Peypouquet (1983) recorded several species of the genus from Neogene horizons at DSDP sites in the western South Atlantic (sites 516, 517, and 518), including two new species (*P. miocenicus* and *P. riograndensis*), but did not mention *P. major* specifically. Whatley & Coles (1987) recorded *Poseidonamicus* sp. cf. *P. major* and *Poseidonamicus* sp. cf. *P. pinto* as ranging late Miocene to Quaternary at DSDP Leg 94 sites in the North Atlantic.

As far as we can gauge from the literature, *P. major* has the following age ranges: south-western Pacific—Miocene to Recent (bathyal–abyssal); south-western Atlantic—Miocene to ?Recent; north-eastern Atlantic—Oligocene; south-western Indian—Recent (abyssal); and, south-eastern Atlantic—Quaternary (abyssal); and North Atlantic, as *Poseidonamicus* cf. *P. major*—late Miocene to Quaternary.

#### Indeterminate taxa

Indet. sp. 62

Fig. 52A–B, D

Two living valves were recovered from sample TBD 3870 at a water depth of 1 026 m. This ovate species has a short, straight DM and prominent anterior and posterior cardinal angles. It has a merodont hinge and a MS pattern consisting of a small rounded anterior scar and three elongate adductors above a smaller oval fourth adductor. It may be related to *Krithe* (R. C. Whatley, pers. comm. 1988).



Indet sp. 23

Fig. 52C

Two fragments of the anterior ends of RV were recovered from sample TBD 3174 at a water depth of 1 050 m. The species has a broadly rounded AM with a narrow, spinose rim. There is a prominent spinose ridge in the antero-ventral region, but otherwise the anterior part of the valve surface is smooth. It may belong in *Bathycythere* (R. C. Whatley, pers. comm. 1988).

## DISCUSSION

A total of 1 023 autochthonous specimens were recovered from 45 sediment samples in water depths greater than 900 m off south-western Africa (only one sample of the original 46 in our data set was barren of ostracods). These represent 31 species, of which four are neritic taxa whose ranges extend 100 m or less into depths that we equate with the Bathyal Zone. The 27 genuinely deep-water species are assigned to 16 genera and two indeterminate categories.

### DEPTH RANGES AND FAUNAL ZONES

Figure 53 shows the depth ranges of all the species we have isolated, and the inset plots the turnover rate (appearances/disappearances) against depth (summed for 100 m intervals). These data indicate that important changes in composition of the ostracod faunas occur within three depth zones: 900–1 100 m; 1 300–1 700 m; and 2 000–2 100 m. (The fourth peak on the right-hand-side of the inset is an artefact caused by the small number of samples available in water deeper than 2 100 m.) Figures 54–56 and Table 7 show further details of these faunal changes and allow us to isolate with more precision the depths at which they occur.

Between 900 m and 1 050 m, ten species appear or disappear, with a further seven species passing through the zone unaffected (Fig. 54). Four of the species that die out are taxa that also occur in relatively shallow water, and have no significant presence in the deep-water faunas; we consider these to be stragglers from the neritic assemblages, and they have not been treated in the taxonomic section of this paper (*Buntonia* sp. 34, *Xestoleberis* sp. nov., *Bythocypris* sp. 42, and *?Bradleya* sp. 56). Considering species that occur in more than one sample (i.e. those for which we can determine a depth range), 57 per cent of the turnover events take place between 950 m and 1 000 m, 29 per cent between 900 m and 950 m, and 14 per cent between 1 000 m and 1 050 m. The appearance and disappearance, respectively, of *Parakrithe* sp. 10 and *?Bradleya* sp. 56 at 945 m suggests that the significant faunal change occurs closer to 950 m than to 1 000 m. It is unlikely, in fact, to occur at a specific depth for individual or all species, but for the purposes of discussion and diagrammatic presentation, we nominally take 950 m as the depth at which the boundary between the neritic and bathyal ostracod assemblages lies. The reality of a major faunal break at approximately this

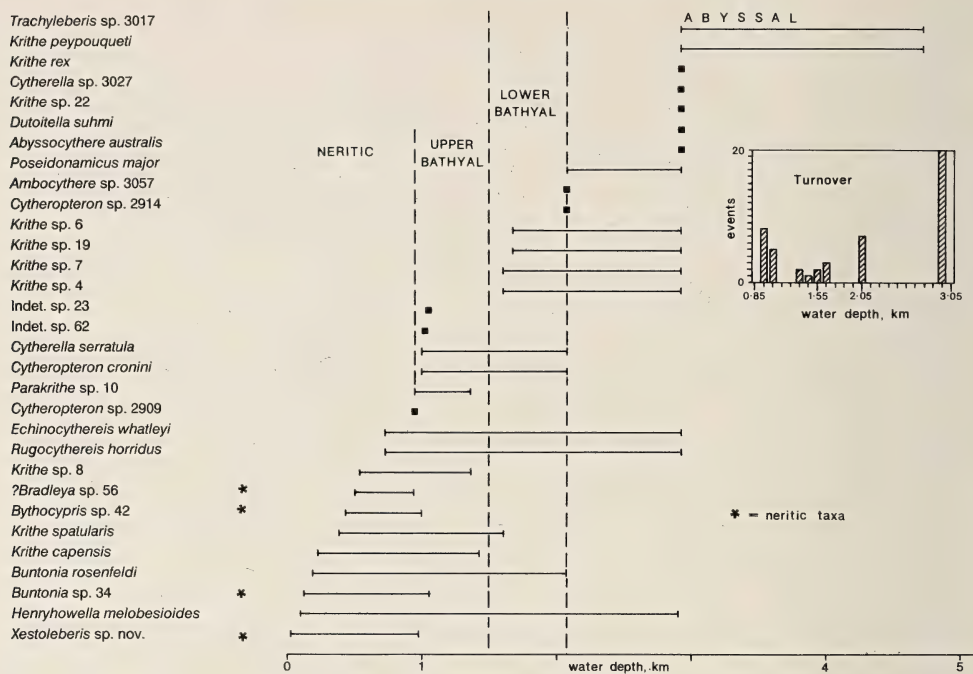


Fig. 53. Depth range chart for Quaternary deep-water ostracods off south-western Africa. Inset shows turnover of appearances and extinctions (events) summed for 100 m intervals with bars centred on the median 50 m depth.

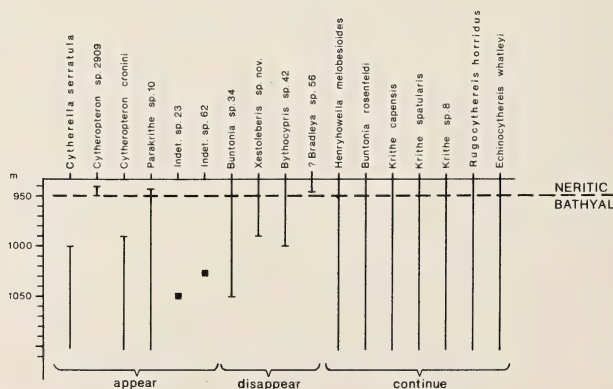


Fig. 54. Depth ranges for species at the Neritic/Bathyal Zone boundary.

depth is also suggested by changes in the abundances of three diagnostic ostracod groups that dominate the deep-water populations (*Henryhowella melobesioides*, *Krithe* spp., and *Buntonia rosenfeldi*—referred to as the HKB assemblage)

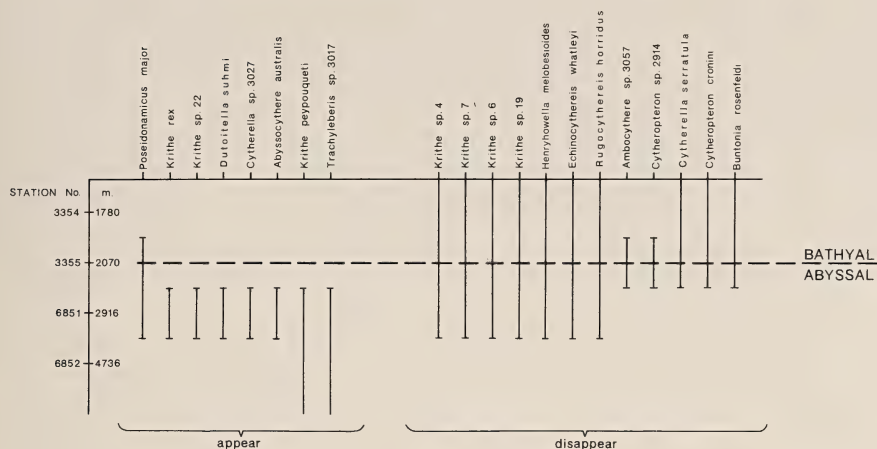


Fig. 55. Depth ranges for species at the Bathyal/Abyssal Zone boundary.

(Fig. 56): the commencement of a sharp decline into deeper water in the abundance of *H. melobesioides*; the temporary reversal of the abundances of *Krithe* spp. and *B. rosenfeldi* relative to each other; and a sharp decline into deeper water in the combined abundance of all three taxa.

The faunal change between 2 000 m and 2 100 m, in fact, relates to one sample (TBD 3355) at 2 070 m, but the size in turnover in the fauna that is defined by this point (8 events), coupled with the apparently coincidental extinction of *Buntonia rosenfeldi* and the appearance of *Poseidonamicus major*, indicate that a major shift in the character of the ostracod population occurs at approximately this level. Thirteen species probably appear or disappear in the 1 200 m interval straddling this depth (Fig. 55), so we nominally take the location of this sample to mark the depth of the boundary between the bathyal and abyssal ostracod assemblages.

The faunal changes that are represented on the inset in Figure 53 by a cluster of turnover events between 1 300 m and 1 700 m are accompanied by a dramatic alteration in the character of the HKB assemblage (Fig. 56). Across this zone, the previously dominant taxon (*H. melobesioides*) rapidly declines in abundance from more than 85 per cent to *c.* 30 per cent of the total ostracod population, whereas *Krithe* spp. progressively, and *B. rosenfeldi* temporarily, become more important. In addition, the contribution to the total ostracod population of the HKB assemblage declines across this zone from more than 95 per cent to *c.* 70 per cent. We nominally take the point at which *H. melobesioides* ceases to be dominant to mark the boundary between these upper and lower bathyal assemblages, viz. 1 500 m.

The vertical changes in the physical properties of the water column off south-western Africa have briefly been mentioned in the introduction, and are



shown in Figure 2. On Figure 56 they have been related to the ostracod distributions, and it is suggested that the important faunal changes described above can be directly correlated with the boundaries between and within the major water masses. Shannon (1966, 1985, figs 11, 12) has plotted the vertical limits of the low salinity zone within the AAIW and, although these fluctuate slightly with latitude, the base lies at approximately 1 000 m. This is close to the depth at which we have located an important change in the composition of the ostracod fauna (950 m), and consequently we suspect that the level of the neritic/bathyal faunal boundary is controlled by the depth of the base of the low salinity zone within the AAIW.

The AAIW is underlain by southward-flowing, low-temperature, high-salinity NADW, and the boundary between these two major water masses lies at approximately 1500 m off south-western Africa (Shannon 1985). This level coincides with the depth at which we have identified important changes in the HKB assemblage, and consequently we suspect that the level of the the upper/lower bathyal faunal boundary is controlled by the depth of the AAIW/NADW shear zone.

Within the NADW mass, Shannon (1985) has located the core at between 2 km and 3 km water depth, and we suggest that the bathyal/abyssal faunal boundary coincides with the top of this zone.

In the Cape Basin, Antarctic Bottom Water (AABW) lies below the NADW in water depths greater than about 4 km (Shannon 1985). It is colder and less saline than the overlying water mass, and its higher dissolved CO<sub>2</sub> values and relatively vigorous circulation are corrosive to carbonate valves (e.g. Tucholke & Embley 1984). The top of the AABW forms the carbonate lysocline, across which the calcareous skeletons of dead organisms are progressively more rapidly dissolved with increasing depth. This is an 'aggressive' physico-chemical environment but, because we have only one sample from below this level (TBD 6852: 4 736 m), we have insufficient data to establish if it coincides with a further change in the ostracod fauna. Certainly, the dead fauna was sparse and poorly preserved but we have no data on the living fauna.

Table 8 summarizes the physical properties of the three major water masses mentioned above.

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Fig. 56. Variations in the abundances of the HKB ostracod assemblage (as % total ostracod fauna) from neritic to abyssal depths. Data are five point running means. Triangles (upper curve) = total assemblage; squares = *Krithe* spp.; diamonds = *Henryhowella melobesioides*; crosses = *Buntonia rosenfeldi*. Lower part of the diagram correlates aspects of the abundance curves with various water mass properties. Zone over which *H. melobesioides* is more than 50 per cent of total ostracod fauna is stippled, and the depths at which it dominates the HKB assemblage are shown as black bars. SMZ = salinity minimum zone; AAIW = Antarctic Intermediate Water mass; NADW = North Atlantic Deep Water mass.

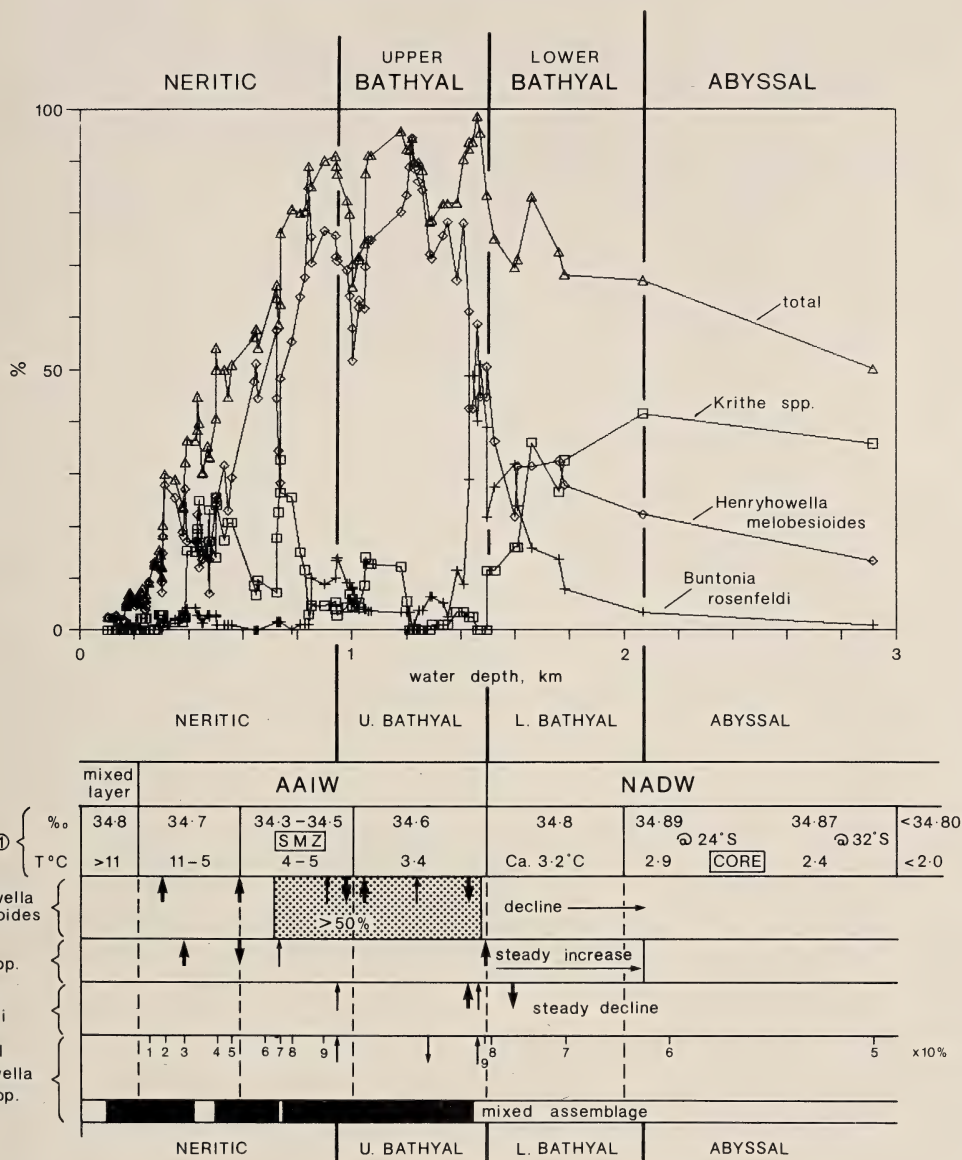


TABLE 7  
Summary of changes at faunal boundaries.

	Species	Depth (m)
Upper limit of Upper Bathyal Zone (950 m)		
Appearance of:	<i>Parakrithe</i> sp. 10	945
	<i>Cytheropteron</i> sp. 2909	945
	<i>Cytheropteron cronini</i>	990
	<i>Cytherella serratula</i>	1 000
	Indeterminate sp. 23	1 050
	Indeterminate sp. 62	1 026
Disappearance of:	<i>Buntonia</i> sp. 34	1 050
	<i>Xestoleberis</i> sp. nov.	1 000
	<i>Bythocypris</i> sp. 42	1 000
	? <i>Bradleya</i> sp. 56A	945
Upper limit of Lower Bathyal Zone (1 500 m)		
Appearance of:	<i>Krithe</i> sp. 7	1 600
	<i>Krithe</i> sp. 4	1 600
	<i>Krithe</i> sp. 6	1 662
	<i>Krithe</i> sp. 19	1 662
Disappearance of:	<i>Krithe capensis</i>	1 430
	<i>Krithe spatularis</i>	1 662
Upper limit of Abyssal Zone (2 070 m)		
Appearance of:	<i>Poseidonamicus major</i>	2 070
	<i>Dutoitella suhmi</i>	2 916
	<i>Trachyleberis</i> sp. 3017	2 916
	<i>Abyssocythere australis</i>	2 916
	<i>Krithe</i> sp. 22	2 916
	<i>Krithe peypouqueti</i>	2 916
	<i>Krithe rex</i>	2 916
	<i>Cytherella</i> sp. 3027	2 916
Disappearance of:	<i>Cytherella serratula</i>	2 070
	<i>Cytheropteron cronini</i>	2 070
	<i>Cytheropteron</i> sp. 2914	2 070
	<i>Buntonia rosenfeldi</i>	2 070
	<i>Ambocythere</i> sp. 3057	2 070

TABLE 8  
South-eastern Atlantic deep-water masses. (Data from Shannon 1985.)

Water mass	Depth (km)	Temperature (°C)	Salinity (‰)	Direction*
Antarctic Intermediate Water (AAIW)	0,2–1,5	11–6	34,7–34,3	NW
Salinity minimum zone	0,6–1,0		34,5–34,3	
North Atlantic Deep Water (NADW)	1,5–4,0	3,2–2,4	34,93–34,87	SE
Antarctic Bottom Water (AABW)	>4,0	<1,5	<34,77	SE

\* direction of flow off south-western Africa.



## BATHYAL FAUNAS

A total of 20 ostracod species has been identified from the Bathyal Zone off south-western Africa, three of which are neritic species at the limits of their depth ranges (Table 9A, Fig. 54).

The fauna of this zone (950–2 070 m) can be considered transitional between the taxonomically diverse (at least 120 species), but geographically endemic, neritic faunas of the continental shelf and upper slope, and the taxonomically relatively restricted (17 species), but cosmopolitan, faunas of abyssal depths. Only eight species are restricted to the Bathyal Zone (Fig. 53) and, of these, five (*Ambocythere* sp. 3057, *Cytheropteron* sp. 2914, *Cytheropteron* sp. 2909, and Indet. spp. 23 and 62) occur at the limits, leaving three species only that range between the base of the AAIW salinity minimum zone and the AAIW/NADW shear zone: *Cytherella serratula*, *Cytheropteron cronini*, and *Parakrithe* sp. 10. In addition, these eight species constitute only 7 per cent of the total bathyal ostracod population. Consequently, the bulk of the fauna is composed of species that range into the over- and underlying zones. Nevertheless, the composition of the fauna of the Bathyal Zone is sufficiently different to distinguish it as an identifiable population that has similarity indices of only 30 per cent and c. 10 per cent with the abyssal and neritic faunas, respectively.

Throughout the Bathyal Zone the HKB assemblage constitutes a minimum of 65 per cent of the ostracod fauna, and over most of the depth range this figure exceeds 70 per cent (Fig. 56). The individual categories are dominated by *Henryhowella melobesioides* (61%), with *Krithe* spp. (13%) and *Buntonia rosenfeldi* (9%) in relatively minor roles (Fig. 57A), but these mean values mask fluctuations across the zone that indicate an important subdivision into upper and lower populations. This change occurs at approximately 1 500 m, above which the total HKB assemblage typically constitutes more than 80 per cent of the fauna and is dominated by *H. melobesioides* (>70%), and below which the HKB assemblage constitutes less than 80 per cent of the fauna and its three constituent taxa are more equally mixed. As we will discuss later, these faunal changes can be correlated with alterations in environmental parameters that define the Upper and Lower Bathyal zones.

The most diverse genus within the Bathyal Zone is *Krithe*, with seven species, but no individual species ranges throughout the zone and there is a marked faunal discontinuity within the genus at the Upper/Lower Bathyal Zone boundary.

## UPPER BATHYAL ZONE

Sixteen ostracod species occur within the Upper Bathyal Zone but three of these are stragglers from the Neritic Zone (Table 9A, Fig. 54). Of the 13 bathyal species, nine (representing 82% of the total fauna) are forms that also occur in shallower depths.

The ostracod faunas of this zone are numerically dominated by the three taxa of the HKB assemblage (Figs 56, 57B). Although together they typically

TABLE 9  
Percentage composition of fauna at bathyal and abyssal depths.

A. Bathyal Zone (950–2 070 m)		Upper (950–1 500) %	Lower (1 500–2 070) %	overall %
<i>Henryhowella melobesioides</i>	#*	65	31	61
<i>Buntonia rosenfeldi</i>	#	8	14	9
<i>Krithe</i> sp. 8	#	4	—	3
<i>Echinocythereis whatleyi</i>	#*	3	8	4
<i>Cytherella serratula</i>		2	9	3
<i>Rugocythereis horridus</i>	#*	2	1	2
<i>Krithe capensis</i>	#	1	—	1
<i>Parakrithe</i> sp. 10		1	—	1
<i>Krithe spatularis</i>	#	1	3	1
<i>Cytheropteron cronini</i>		1	1	1
<i>Cytheropteron</i> sp. 2909		0,1	—	0,1
Indeterminate sp. 23		1	—	1
Indeterminate sp. 62		1	—	1
Indeterminate fragments		—	4	0,1
<i>Krithe</i> sp. 4	*	—	9	1
<i>Krithe</i> sp. 6	*	—	1	0,1
<i>Krithe</i> sp. 7	*	—	3	0,1
<i>Krithe</i> sp. 19	*	—	5	1
<i>Ambocythere</i> sp. 3057		—	3	0,1
<i>Cytheropteron</i> sp. 2914		—	0,1	0,1
<i>Poseidonamicus major</i>	*	—	5	1
Total for <i>Krithe</i> spp.		6	21	7
Neritic forms (at lower limit of their depth range)				
<i>Buntonia</i> sp. 34		8	—	7
<i>Xestoleberis</i> sp. 35		1	—	1
<i>Bythocypris</i> sp. 42		1	—	1
B. Abyssal Zone		TBD 6851 (2 916 m) %	% <i>Krithe</i>	
<i>Poseidonamicus major</i>	*	29		
<i>Krithe rex</i>		3	6	
<i>Krithe peypouqueti</i>		13	28	
<i>Henryhowella melobesioides</i>	*	6		
<i>Dutoitella suhmi</i>		6		
<i>Abyssocythere australis</i>		6		
<i>Krithe</i> sp. 4	*	6	13	
<i>Krithe</i> sp. 7	*	5	11	
<i>Krithe</i> sp. 6	*	7	15	
<i>Krithe</i> sp. 19	*	4	8	
<i>Krithe</i> sp. 22		6	12	
Indeterminate <i>Krithe</i>		3	6	
Total <i>Krithe</i> spp.		47	100	
<i>Rugocythereis horridus</i>	*	2		
<i>Echinocythereis whatleyi</i>	*	1		
<i>Trachyleberis</i> sp. 3017		1		
<i>Bradleya</i> sp. 56		1		
<i>Cytherella</i> sp. 3027		0,1		
Indeterminate fragment		0,1		
17 species, 354 valves, diversity of 5 per cent				

\* = common to bathyal and abyssal faunas; # = common to bathyal and neritic faunas  
Note: Percentages are based on total number of valves per zone, and not merely the number of valves in those samples in which a particular species occurs.

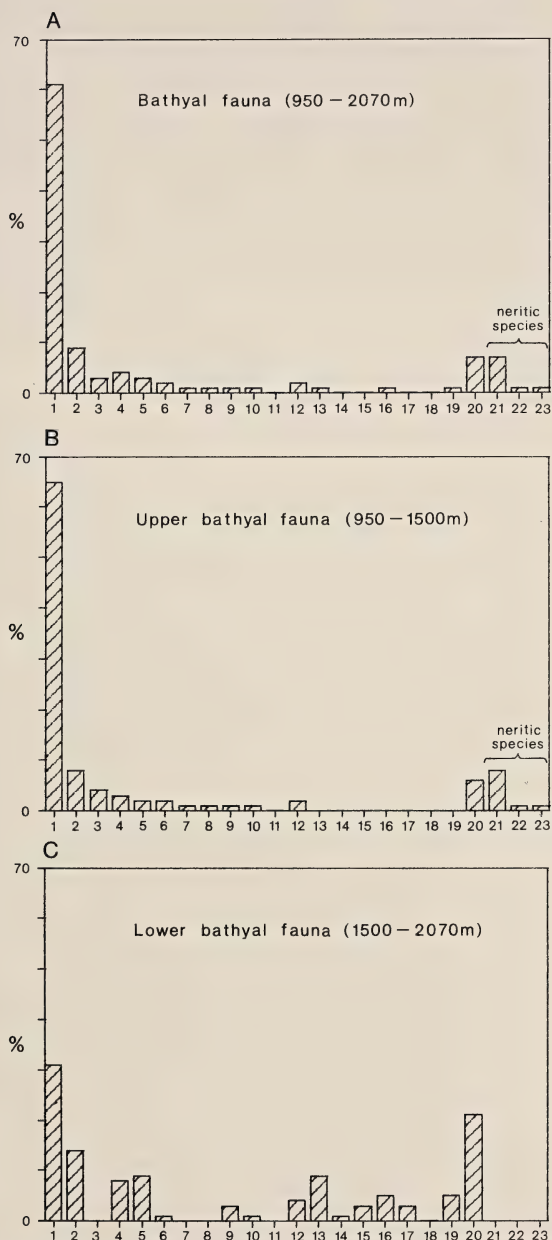


Fig. 57. Species histograms (percentage of total ostracod fauna) for whole Bathyal (A), Upper Bathyal (B), and Lower Bathyal (C) zones. Species identification: 1—*Henryhowella melobesioides*; 2—*Buntonia rosenfeldi*; 3—*Kriithe* sp.8; 4—*Echinocythereis whatleyi*; 5—*Cytherella serratula*; 6—*Rugocythereis horridus*; 7—*Kriithe capensis*; 8—*Parakriithe* sp. 10; 9—*Kriithe spatularis*; 10—*Cytheropteron cronini*; 11—*Cytheropteron* sp. 2909; 12—Indeterminate species; 13—*Kriithe* sp. 4; 14—*Kriithe* sp. 6; 15—*Kriithe* sp. 7; 16—*Kriithe* sp. 19; 17—*Amboocythere* sp. 3057; 18—*Cytheropteron* sp. 2914; 19—*Poseidonamicus major*; 20—total *Kriithe* spp.; 21—*Buntonia* sp. 34; 22—*Xestoleberis* sp. nov.; 23—*Bythocypris* sp. 42.



constitute more than 80 per cent of the population, there is considerable variation across the zone from less than 70 per cent immediately below the upper boundary, to more than 90 per cent at 1,2 km and 1,45 km. These fluctuations, to a large extent, reflect the changes in abundance of *Henryhowella melobesioides*, which is the dominant taxon in the Upper Bathyal Zone. This species becomes progressively more abundant with increasing depth down the continental slope and reaches a peak (c. 75%) within the salinity minimum zone at the base of the Neritic Zone. It suffers a sharp, but temporary, decline at the top of the Upper Bathyal Zone but, with increasing depth, has a second abundance peak between 1 200 m and 1 300 m (>80%). Below this depth its importance rapidly declines, particularly across the Upper/Lower Bathyal boundary.

Both *Krithe* spp. (6%) and *Buntonia rosenfeldi* (8%) are relatively minor components of the HKB assemblage in the Upper Bathyal Zone, in terms of overall abundance (Fig. 57B), but at particular depths are temporarily more abundant, where they respond to certain environmental factors. In the case of *B. rosenfeldi*, this occurs across the Upper/Lower Bathyal boundary (and in the salinity minimum zone at the base of the Neritic Zone), whereas *Krithe* species become more abundant immediately below the base of the salinity minimum zone in the AAIW (Fig. 56).

The three species of *Krithe* that occur within the Upper Bathyal Zone (Upper *Krithe* Fauna) are all inherited from the overlying Neritic Zone (Figs 11, 13, 53). Their variations in relative abundance can be correlated with changes in environmental parameters (see next section), and allow a zonation of the Upper Bathyal Zone. *Krithe capensis* is the dominant species within the Neritic Zone but rapidly declines in abundance across the Neritic/Bathyal boundary, below which it is replaced by *Krithe* sp. 8. The latter in turn is replaced by *K. spatularis* in depths greater than approximately 1 000 m. Of the three Upper Bathyal Zone species of *Krithe*, only *K. spatularis* extends across the AAIW/NADW shear zone into the Lower Bathyal Zone, but it dies out near the top, where it is replaced by the four species of the Lower *Krithe* Fauna.

Within the minor elements of the bathyal ostracod fauna, several species appear near the top of the Bathyal Zone, although only three have an extended range into deeper water, and of these only *Parakrithe* sp. 10 is confined to the Upper Bathyal Zone. *Cytherella serratula* is the sole representative of the genus within the Bathyal Zone, and is only relatively abundant either side of the Upper/Lower boundary, where it appears to favour the unstable physico-chemical environments associated with the shear zone. Across the continental margin off south-western Africa, the genus *Cytheropteron* is as diverse as *Krithe* (12 spp.), but the majority of its species are confined to the shelf and upper slope (see Fig. 8). Deep-water representatives are confined to three species, but only *Cytheropteron cronini* has been found over a wide depth range. Finally, *Echinocythereis whatleyi* and *Rugocythereis horridus* are both characteristic members of the Upper Bathyal Zone fauna and, although the latter has its

highest abundance within this zone, neither is numerically important, except within individual samples.

#### LOWER BATHYAL ZONE

Fourteen species have been recovered from the Lower Bathyal Zone, 50 per cent of which extend into the Upper Bathyal Zone, 57 per cent extend into the Abyssal Zone, and 36 per cent extend into the Neritic Zone (Tables 9, 10). The character of the Lower Bathyal Zone fauna contrasts strongly with that of the Upper Bathyal Zone fauna by having a mixed *Henryhowella melobesioides*/*Krithe* spp./*Buntonia rosenfeldi* assemblage, as opposed to one dominated by *H. melobesioides* (Figs 56, 57C). In terms of total specimens recovered from the Lower Bathyal Zone, *H. melobesioides* is the most important species (31%) but, except for isolated samples, it is subordinate in abundance to one or other of the two other taxa. In addition, with increasing water depth *H. melobesioides* becomes progressively less important, whereas *Krithe* species steadily become more abundant and diverse (Figs 11, 13), with the appearance of four species in the top part of the zone. Including *K. spatularis*, which extends downwards from the Upper Bathyal Zone, 36 per cent of the species recorded from the Lower Bathyal Zone belong to the genus *Krithe*. The most abundant of these is *Krithe* sp. 4.

*Buntonia rosenfeldi* occupies a transitional position in the switch from *H. melobesioides* to *Krithe* spp. dominated faunas at the Upper/Lower Bathyal Zone boundary, by temporary increases in abundance at water depths where *H. melobesioides* declines but where *Krithe* spp. do not expand to fill the environmental niches. This opportunistic expansion is also displayed by *Echinocythereis whatleyi* and to a lesser extent by *Cytherella serratula*, both of which show marked increases in abundance at approximately the same levels as *B. rosenfeldi*.

The depth at which we nominally take the Lower Bathyal/Abyssal Zone boundary (2 070 m) coincides with our first record of the species *Poseidonamicus major*, which is the link to the typical abyssal assemblage in sample TBD 6581. This is also the deepest occurrence of several of the bathyal species—*Buntonia rosenfeldi*, *Cytherella serratula*, and *Cytheropteron cronini*—and the sole record of two rare taxa, *Ambocythere* sp. 3057 and *Cytheropteron* sp. 2914.

#### ABYSSAL FAUNAS

It is in the Abyssal Zone that the true deep-water, cosmopolitan ostracod faunas are encountered. The character of the population is markedly different from that found in the Bathyal Zone and the fauna is dominated by various species of the genus *Krithe* (8 species), which combined comprise 47 per cent of the ostracod population in our largest sample (TBD 6851, 2 916 m, 354 valves). The most abundant single species are *Poseidonamicus major* (29%) and *Krithe peypouqueti* (13%), with the overall importance of the HKB assemblage within the total ostracod population showing a steady decline from the upper part of

TABLE 10  
Comparison of Upper Bathyal, Lower Bathyal and Abyssal faunas.

## A. SIMILARITY

Upper Bathyal*	Lower Bathyal	Abyssal
13 species	14 species	17 species
20 species, 7 common similarity = 35%		24 species, 8 common similarity = 33%
Bathyal		Abyssal
20 species		17 species
27 species, 8 common similarity = 30%		

$$\text{Similarity} = \frac{\text{No. species common to both units}}{\text{Total no. different species in both units}} \times 100$$

$$= \frac{\text{common}}{\text{species}} \times 100$$

\* — values do not include the three neritic taxa

## B. PERCENTAGE SPECIES COMMON

	Abyssal	Lower Bathyal	Upper Bathyal	Neritic <sup>§</sup>
Abyssal	—	47	29	24
Lower Bathyal	57	—	50	36
Upper Bathyal	23	54	—	69
Neritic <sup>§</sup>	<1	<1	1	—

<sup>§</sup> = No. of neritic species taken as 120 (unpublished data).

Examples:

What percentage of Upper Bathyal species occur in the Lower Bathyal Zone? ... 54

What percentage of Lower Bathyal species occur in the Upper Bathyal Zone? ... 50

the Abyssal Zone (65% at 2 070 m) into deeper water (50% at 2 916 m), in which depths *Buntonia rosenfeldi* does not occur.

Forty-seven per cent of the abyssal species are endemic to the Abyssal Zone, which contrasts strongly with 31 per cent and 14 per cent endemism for



the Upper and Lower Bathyal Zones, respectively. In addition, several of the genera do not presently occur in the shallower zones off south-western Africa: *Trachyleberis* (? = *Legitimocythere*), *Abyssocythere*, and *Dutoitella*. All of the *Kriethe* species that comprise the Lower *Kriethe* Fauna, and which appear beneath the AAIW/NADW boundary in the Lower Bathyal Zone, persist into the Abyssal Zone, but they are subordinate in abundance to the abyssal endemic *K. peypouqueti*. *Rugocythereis horridus* and *Echinocythereis whatleyi* also occur in the Abyssal Zone but form only minor elements of the overall population (2% and 1%, respectively).

Our deepest sample (TBD 6852, 4 736 m) lies beneath the carbonate compensation depth, and contains a sparse fauna of *Kriethe peypouqueti* and *Trachyleberis* sp. 3017 that shows signs of dissolution. This is the only record we have of the ostracod fauna within the AABW mass, which is such an important feature of the circulation in the Cape Basin and has vigorously scoured or maintained an omission surface in the region since at least late Miocene time (Embley & Tucholke 1984; Dingle *et al.* 1987). Preservation of the shallower assemblages within the overlying NADW is generally good.

#### SEDIMENTARY AND OCEANOGRAPHIC ENVIRONMENTS

The studies of Rosenfeld & Bein (1978), Cronin (1983), and Benson *et al.* (1983) on the ostracod faunas of the continental margins off north-western Africa and eastern North America, suggest that variations in dissolved oxygen, salinity, and temperature are the main factors in determining the water-depth ranges of individual deep-sea species. We will assess the influence of these parameters on the faunas off south-western Africa, and then briefly compare our results with their work.

#### OSTRACOD ABUNDANCE AND WATER DEPTH

The only physical parameter that is directly linked to water depth is hydrostatic pressure. All other factors that are likely to limit the vertical distribution of ostracods (e.g. temperature, salinity, dissolved O<sub>2</sub> and CO<sub>2</sub>, nutrients, light, substrate, etc.) vary with depth only through a general vertical zonation imposed by the structure of the water column. Nevertheless, within any area, the latter phenomenon will maintain a relatively steady-state depth-related population structure that allows a vertical zonation based on either assemblages or individual species. Projecting such depth-zonations to other areas must, by definition, be attempted with caution. Murray (1973: 168) discussed the same problem in relation to benthic foraminifera and concluded '... that depth zones recognized in one area on the basis of certain indicator species are only applicable to that area and to adjacent areas where the environmental conditions are essentially the same'. However, because globally there are fundamental similarities in the vertical structuring of the deep water masses, a similar, relative depth-related succession of ostracod taxa can be anticipated world-wide.

Figure 58A shows the variation in abundance of ostracods (measured as number of valves per 100 g of the original, dry sediment sample) on the continental margin off south-western Africa. The highest abundances ( $>500$  valves/100 g) all lie on the continental shelf ( $<220$  m water depth, above the thermocline), with the majority of sites on the slope containing less than 100 valves/100 g (mean = 29). There is a cluster of higher values ( $>100$ ) either side of 400 m water depth, and a further 'peak' (up to 230 valves/100 g; mean = 98) at the base of the AAIW salinity minimum zone (Neritic/Bathyal Zone boundary). Otherwise, maximum values for the Upper Bathyal Zone lie between 40 and 50 valves/100 g (mean = 24) (Fig. 58B). Between 1 450 m and 1 500 m, immediately above the AAIW/NADW shear zone (i.e. the Upper/Lower Bathyal boundary), values drop to less than 10 valves/100 g, and recover only to 15–20 valves/100 g between this level and our deepest data point at 1 780 m.

These data suggest that there is no relationship between variation in ostracod abundance and water depth, but there is strong correlation between variations in abundance and structure of the water masses.

#### OSTRACOD ABUNDANCE AND MUD CONTENT OF SEDIMENTS

The mud (silt and clay:  $<63$  micron) content of 218 sediment samples from the continental margin off south-western Africa is plotted against water depth in Figure 59. There is a general increase in the mud content of sediments with increasing depth from the continental shelf to 1 km, both in terms of number of samples with more than 50 per cent mud content, and in mean percentage mud. However, although the former parameter maintains a value of more than 90 per cent in depths greater than 1 km, the mean percentage mud content of the sediments reaches a high of 84 per cent at 1 km, but decreases slightly farther downslope (to 80% at 1,7 km). Mean percentage mud values for the various zones are: Neritic—49 per cent; Upper Bathyal—82 per cent, Lower Bathyal—82 per cent.

A comparison of Figures 58A–B (details of the mean percentage mud and ostracod abundance for the Bathyal Zone), 59 and 60 (scattergrams of percentage mud plotted against ostracod abundance as valves/100g), reveals the following trends:

1. Ostracod abundances on the continental margin off south-western Africa are greatest ( $>500$  valves/100 g) on the mid to outer continental shelf (150–220 m water depth). Although the mean mud content of the sediments in this depth range is less than 50 per cent, all the samples with abundances greater than 300 valves/100 g occur in samples with a mud content of more than 50 per cent. This indicates that the mud content of the shelf samples is very variable but that ostracods are most abundant in muddy samples, with maximum populations (up to 1 900 valves/100 g) occurring in sediments with mud contents between 75 and 90 per cent (Fig. 60A). Until we have studied these faunas in detail, we cannot comment on the specific diversity of such populations.

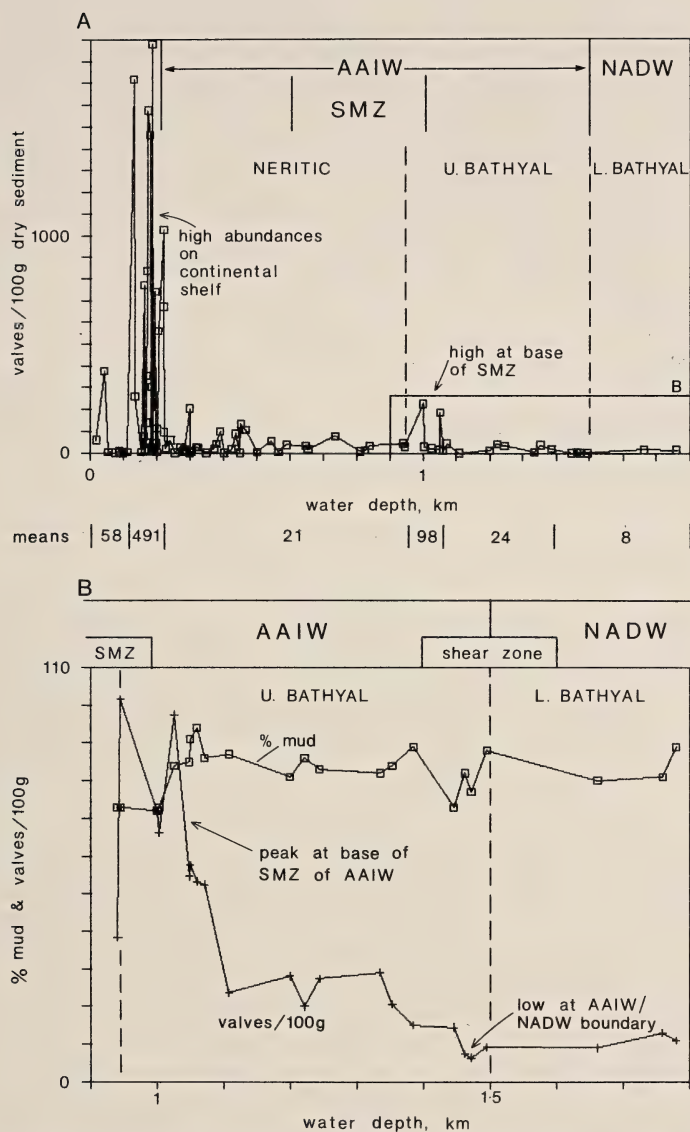


Fig. 58. Relationship between ostracod abundance, water depth, and mud content of sediments. A. Abundance of ostracods (number of valves per 100 g of dry, unprocessed sediment) plotted against sample depth (number of samples = 101). Mean values for various depth ranges are recorded below the horizontal axis. The rectangular block in the lower right corner outlines the data field used in Fig. 58B. B. Percentage mud and number of ostracod valves/100 g (both five point running means) plotted against water depth in the Upper and Lower Bathyal zones. Mud values are from Fig. 59, valve numbers from Fig. 58A. N.B. Values on the vertical axis refer to '% mud' and 'valves/100 g'.



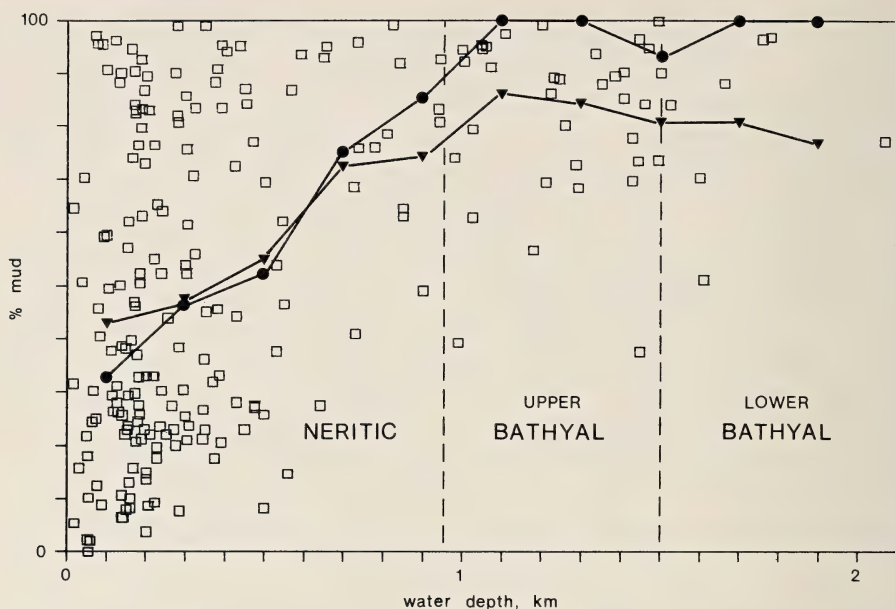


Fig. 59. Variation of mud content (silt and clay) with water depth for 218 sediment samples from the continental margin of south-western Africa. The two curves plot data summed over 200 m intervals: circles = % of samples which have mud values >50%; triangles = mean % mud: values are plotted at median depth point (e.g. data for the 0–200 m interval are plotted at 100 m level). Mud values are from Birch (1975), Rogers (1977) and Bremner (1981).

2. On the upper continental slope (water depths between 223 m and 900 m), the mean ostracod abundance is 29 valves/100 g, whereas the mean mud content steadily increases to more than 70 per cent, so that in this region the sympathetic relationship between high mud values and high population numbers that we detect on the shelf does not hold.

3. At the base of the salinity minimum zone (SMZ)/bathyal thermocline of the AAIW mass (i.e. at the Neritic/Upper Bathyal Zone boundary), there is a narrow zone (c. 950–1 050 m) of high ostracod abundance (mean = 98 valves/100 g). The mean percentage mud value for the 800–1 000 m interval is 74 per cent, but where it rises to 85 per cent in the underlying 200 m wide sector, the ostracod abundances decline significantly (mean = 24 valves/100 g—Fig. 58B). A further decline in abundance occurs in the lowermost Upper Bathyal and Lower Bathyal zones (mean = 8), whereas in the same interval the mean mud values decline slightly (84–77%, and in detail hover around a plateau of about 80%). In general, therefore, although the mud content of the Bathyal Zone sediments is high (>80%—Fig. 60), the ostracod abundances are low overall (<40 valves/100 g), and even the larger populations are relatively small in comparison with those on the continental shelf.

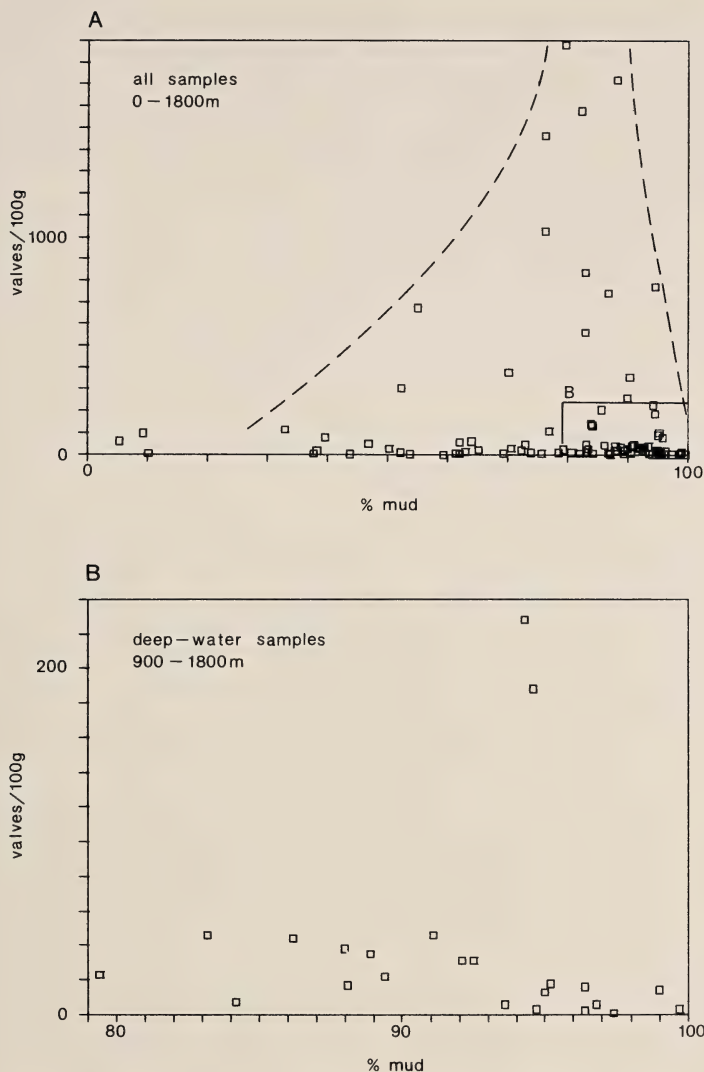


Fig. 60. Number of ostracod valves/100 g plotted against mud content of sample. The total ostracod fauna has been used. A. Samples from a water depth range of 0-1 800 m. The rectangular block in the lower right corner outlines the data field used in Fig. 60B. B. Samples from a water depth range of 900-1 800 m.

Taken together, the data on total ostracod population abundances in relation to water depth and mud content of sediments suggest that, in water depths greater than approximately 200 m, variations in overall abundance are not directly related to the mud content of the sea-floor sediments but are controlled by the structure of the water column. In as much as changes in the water

column will also influence the mud content of the sediments, locally there is a sympathetic relationship in alterations in mud content and overall ostracod abundance. On the continental shelf (above the thermocline and within the influence of surface currents), there is a direct correlation between mud content and total population abundance, but this is a topic we will address in a later contribution on the shallow-water faunas.

The above observations are based on data that monitor variations in the total ostracod population, but these may mask correlations for individual species. In Figure 61A–C, we have plotted the abundance (as percentage total ostracod population) against mud content of sediments for the three taxa in the HKB assemblage and, in Figure 61D, have summarized the percentage of records for each species that occurs in successive 20 per cent mud categories. From these data, we conclude that all three taxa have a preference for sediments with a mud content of more than 50 per cent but that the occurrences of *Henryhowella melobesioides* and *Krihe* spp. are more mud-specific (57% and 55% of records occur in sediments with >60% mud, respectively) than *Buntonia rosenfeldi* (48%). However, the latter has a lower tolerance of low mud contents. We did not record *Buntonia rosenfeldi* in sediments with less than 20 per cent mud, whereas 7 per cent and 3 per cent respectively of occurrences of *H. melobesioides* and *Krihe* spp. were within this category. Further, *B. rosenfeldi* appears to tolerate mud contents of more than 85 per cent less well than either of the other two species. Its abundance (as percentage of total ostracod population) in this category is never more than 25 per cent, whereas in very muddy sediments both *H. melobesioides* and *Krihe* spp. are frequently the dominant taxa. This is especially the case with *H. melobesioides*.

From this brief survey we can conclude that, although the abundance of the overall ostracod population is less influenced by the mud content of the bottom sediments than by factors associated with the ambient water mass, individual species are so influenced.

#### OCEANOGRAPHIC FACTORS

Figure 62 summarizes the vertical changes in dissolved oxygen, salinity, and temperature in transects across the continental margin off south-western Africa. Using these profiles in conjunction with the vertical distribution of selected ostracod taxa (Fig. 63) and variations in the composition of the overall fauna (Figs 53, 56), we can assess the effectiveness of vertical changes in the physico-chemical properties of the water column as barriers to ostracod distribution, and hence the maintenance of the composition of the faunas of the various depth zones.

On the continental shelf, temperature and salinity values are relatively high (>12°C and >34.9‰, respectively) and sediment textures variable. In addition, the pattern of dissolved oxygen values is complicated, with a single minimum zone in the south (Stander 1964), and a double minimum in the north (Chapman & Shannon 1985), with the result that the ostracods of this shallow zone have



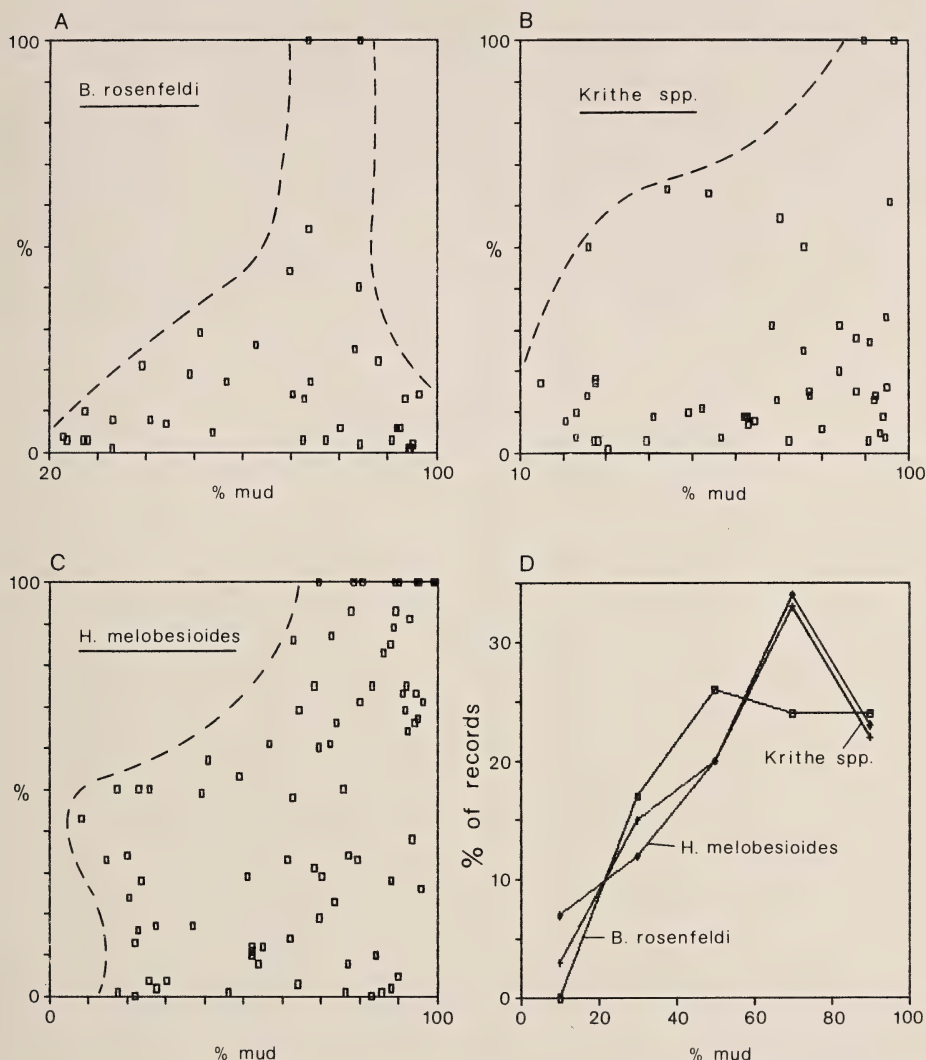


Fig. 61. Abundance of individual species (as % total ostracod fauna) of the HKB assemblage plotted against mud content of samples. A. *Buntonia rosenfeldi*. B. *Krithe* spp. C. *Henryhowella melobesioides*. D. Summary of variation of abundance versus percentage mud for the three species. Values are shown as percentage of records within successive 20 per cent intervals of mud, and have been equalized to avoid sampling bias.

a complex distribution pattern. We will be describing these faunas in a later publication and defer further discussion of this zone until then.

The top of the AAIW mass lies at about 200 m (Shannon 1966, 1985) and is associated with a relatively thick thermocline that is steepest between approximately 200 m and 400 m. At the top of the AAIW, water temperatures vary

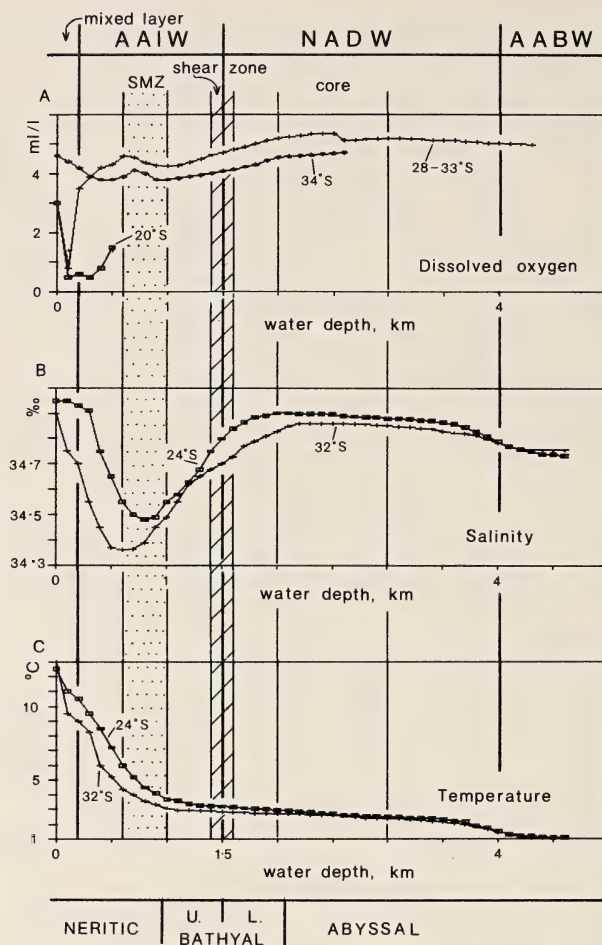
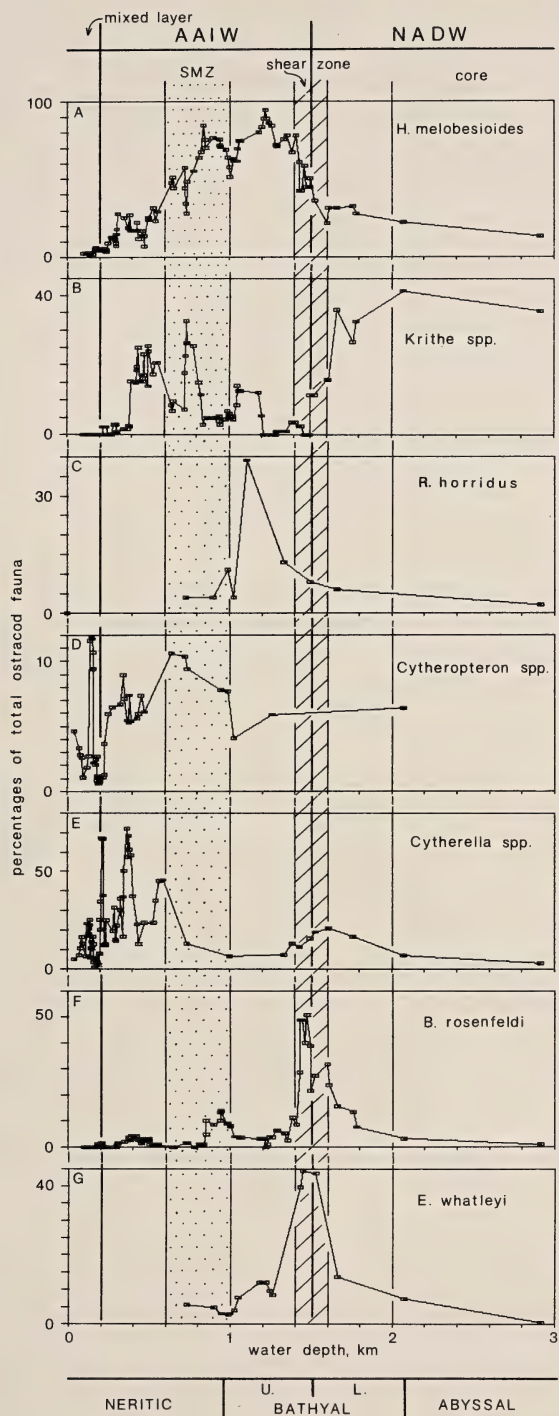


Fig. 62. Variations in physico-chemical parameters on the sea floor along transects off south-western Africa. Water-column structure and faunal zones are correlated along the top and bottom margins of the diagram, respectively. A. Dissolved oxygen ( $\text{ml/l}$ ) at  $20^\circ\text{S}$ ,  $34^\circ\text{S}$ , and a composite profile between  $28^\circ\text{S}$  and  $33.5^\circ\text{S}$  (the deflection in the curve at 2.5 km is an artefact caused by juxtaposition of data from two transects). B. Salinity ( $\text{‰}$ ) at  $24^\circ\text{S}$  and  $32^\circ\text{S}$ . C. Temperature ( $^\circ\text{C}$ ) at  $24^\circ\text{S}$  and  $32^\circ\text{S}$ . Constructed with data from Fuglister (1960), Stander (1964), Bubnov (1966), Shannon & Van Rijswijk (1969), Welsh & Visser (1970), Gorshkov (1978), Shannon (1985), and Chapman & Shannon (1985). Data points taken at 100 m intervals. Zones have been shaded to aid correlation.

Fig. 63 (see facing page). Variations in abundance (% total ostracod population) of various ostracod species correlated with water column barriers, and faunal zones. A—*Henryhowella melobesioides* (five-point means); B—*Krithe* species (five-point means); C—*Rugocythereis horridus* (raw data); D—*Cytheropteron* species (five-point means); E—*Cytherella* species (five-point means); —*Buntonia rosenfeldi* (five-point means); G—*Echinocythereis whatleyi* (three-point means).





from north to south between 11°C and 9°C, and these fall to c. 3,4°C at the base. The gradient of the temperature changes is very low below 1 000 m but increases steadily into shallower water, with the main temperature 'break' at about 3,5°C. This bathyal thermocline approximately coincides with the base of the salinity minimum zone (SMZ) at the core of the AAIW mass (Shannon 1966, 1985), which itself is a relatively low salinity body of water sandwiched between the higher salinity continental shelf waters and the NADW mass (Fig. 62). The lower limit of the SMZ lies at about 1 000 m along the whole of the continental margin off south-western Africa and coincides with a dissolved oxygen minimum zone in which values vary from 4,25 ml/l at 30°S to 3,8 ml/l at 34°S (Fig. 62A). The SMZ is thicker in the south (32°S), where the upper limit occurs at about 500 m, in comparison with 600 m at 24°S. Minimum salinity values in the SMZ vary from 34,36‰ in the south to 34,48‰ in the north. The physico-chemical hiatus that controls the depth of the Neritic/Bathyal Zone boundary appears, therefore, to be a combination of the bathyal thermocline (below which the water temperature is <3,5°C), a steep increase in salinity below the SMZ (with the 'critical' level around 34,50‰), and an oxygen minimum zone.

The boundary between the AAIW and NADW masses lies at about 1 500 m off south-western Africa (Shannon 1985). There is no apparent change in either the temperature or salinity gradients across the contact but, because these bodies are flowing in opposite directions, there will be a relatively intense zone of shearing across it (marked by turbulence and a sharp velocity gradient). The slightly lower mud values detected between 1 400 m and 1 500 m (Fig. 58B) may be related to turbulence in the lowermost part of the AAIW. Variability in temperature, salinity and current strengths, rather than significant breaks in their gradients, seem to be the main factors controlling the location of the Upper/Lower Bathyal zone faunal boundary.

The core of the NADW lies between 2 000 m and 3 000 m (Shannon 1985) and its upper boundary is marked by a sharp change in the salinity values, where the gradient decreases rapidly and below which salinity values peak at about 34,9‰ in the north and 34,86‰ in the south. Below the depths at which these peaks occur (2 000 m and 2 300 m, respectively), the salinity values decrease very slowly. There are no accompanying temperature changes at the top of the NADW core, so that the Bathyal/Abyssal Zone faunal boundary that is maintained by this feature must be related to the relatively large upslope decrease in salinity and any water turbulence that is caused by the velocity gradient across the top of the NADW core zone.

The NADW/AABW boundary lies at about 4 000 m and is marked by small, but significant, increases in both temperature and salinity gradients. Because we have no ostracod-rich samples below 4 000 m, we cannot comment on whether or not this water-mass contact causes a significant faunal hiatus. Certainly, because the top of the AABW mass marks the upper limit of the

carbonate lysocline, the chemical environment below this depth can be expected to be severe.

To assess the effectiveness of these boundaries as barriers to the habitats of various ostracod species, we have plotted the abundances of the numerically most important species and genera against depth (Fig. 63), and can extract the following salient points.

### 1. Base of salinity minimum zone/bathyal thermocline of AAIW

EFFECTIVE: *Krithe* spp. (including *Parakrithe*)—there is a decrease in abundance of the overall population into and out of the SMZ, with a mid-zone high. Two species turn over at lower boundary.

*Cytherella* spp.—very effective barrier; high abundances and number of species in Neritic Zone do not persist across SMZ; bathyal species are isolated by barrier.

*Echinocythereis whatleyi*—does not range above SMZ.

*Rugocythereis horridus*—does not range above SMZ.

*Cytheropteron*—ranges of individual species restrained by SMZ, but not effective in altering overall population abundances, which reach a high in the SMZ.

INEFFECTIVE: *Henryhowella melobesioides*—the drop in abundance at base of SMZ may be related to a decrease in mud content.

*Buntonia rosenfeldi*—favours the conditions therein and reaches a minor peak of abundance just above base of SMZ.

### 2. Boundary of AAIW and NADW masses (shear zone)

EFFECTIVE: *Henryhowella melobesioides*—very effective; dramatic decrease of abundance into NADW.

*Krithe* species—very effective; dramatic increase in abundance into NADW; high species turnover.

*Rugocythereis horridus*—confines high abundances to the Upper Bathyal Zone.

INEFFECTIVE: *Buntonia rosenfeldi*—reaches peak abundance in the shear zone.

*Cytherella* species—*C. serratula* reaches maximum abundance in the shear zone.

*Echinocythereis whatleyi*—reaches maximum abundance in the shear zone.

*Cytheropteron* species—no significant changes across this barrier.

### 3. Top of NADW core

EFFECTIVE: *Krithe* species—small abundance change across barrier, but apparently no turnover of species.

*Buntonia rosenfeldi*—is severely restricted below boundary.

*Cytherella* species—severely restricted below boundary.

*Echinocythereis whatleyi*—abundances low beneath barrier.

*Rugocythereis horridus*—abundances low beneath barrier.

*Cytheropteron* species—*C. cronini* does not range below barrier.

*Poseidonamicus major*—does not range above barrier.

INEFFECTIVE: *Henryhowella melobesioides*—no significant change in abundance across barrier.

Table 11 lists the barriers and the responses to them by individual species. We can summarize the physico-chemical features of each barrier and how it maintains the character of the various faunal zones as follows:

1. Neritic/Upper Bathyal Zone boundary (AAIW—base of SMZ/bathyal thermocline). This barrier consists of: (a) change in temperature gradient ('critical' temperature *c.* 3,5°C); (b) steep salinity gradient (i.e. a zone of rapid change); and (c) oxygen low zone; and has the following effects: (a) prevents the neritic populations of the diverse genera *Cytheropteron*, *Buntonia*, and *Cytherella* from moving downslope and (b) prevents *Rugocythereis horridus* and *Echinocythereis whatleyi* from moving upslope.
2. Upper/Lower Bathyal Zone boundary (AAIW/NADW contact and associated shear zone). This barrier consists of turbulence, resulting in variable tempera-

TABLE 11  
Summary of barrier effectiveness.

		SMZ	AAIW/ NADW	NADW core
Approximate 'critical' parameters	Temp. (°C) Salinity (‰) Oxygen	4,0–3,4 34,5 O <sub>2</sub> low	3,2–3,0 34,8–34,7	3,0–2,7 34,89–34,86
<i>Henryhowella melobesioides</i>			*1	
<i>Krihe</i> spp.		*6	*4	*4
<i>Buntonia rosenfeldi</i>				*2
<i>Cytherella</i> spp.		*3		*2
<i>Echinocythereis whatleyi</i>		*5		*2
<i>Rugocythereis horridus</i>		*5	*1	*2
<i>Cytheropteron</i> spp.		*3		*2
<i>Poseidonamicus major</i>				*4

\* — effective barrier

moving from shallow to deeper depths, cannot tolerate:

<sup>1</sup> — lower temperature and higher salinity

<sup>2</sup> — low temperature and high salinity

<sup>3</sup> — lower temperature and low oxygen

moving from deep to shallower depths, cannot tolerate:

<sup>4</sup> — higher temperature and lower salinity

<sup>5</sup> — higher temperature, higher salinity, and low oxygen

<sup>6</sup> — isolated peak in SMZ

Ranges in 'critical' parameters relate to north to south variations



tures, salinities and current strengths, and has the following effects: (a) separates the *Henryhowella melobesioides*-dominated Upper Bathyal fauna from the mixed *H. melobesioides*/*Krithe* spp./*Buntonia rosenfeldi* Lower Bathyal fauna; (b) limits the depth ranges of several *Krithe* species to produce the Upper and Lower *Krithe* faunas; and (c) allows three species to opportunistically increase their abundances—*Buntonia rosenfeldi*, *Cytherella serratula*, and *Echinocythereis whatleyi*.

3. Lower Bathyal/Abyssal Zone boundary (top of NADW core). This barrier consists of: (a) change in salinity gradient ('critical' salinity c. 34,89‰ in the north and 34,86‰ in the south); and (b) ?turbulence, and has the following effects: (a) maintains peak *Krithe* spp. population abundances downslope; (b) prevents *Buntonia rosenfeldi* and *Cytheropteron cronini* from extending farther downslope; (c) prevents *Poseidonamicus major* from extending farther upslope. This regulates the upper level of a true abyssal taxon.

Finally, it is clear that, although we have been able to identify the efficiency of these physico-chemical changes in the water column as regulators of overall faunal character, the taxa involved react to these changes in different ways. To some they are solid barriers and to others sieves, and it is not possible at this stage to identify a predictable pattern.

A particularly good example of this apparently random response occurs at the AAIW/NADW shear zone. Here, within what we can only tentatively suggest is a narrow, turbulent layer of mixed water with variable temperatures, salinities, and current strengths, there are relatively large increases in abundances of *Buntonia rosenfeldi*, *Cytherella serratula*, and *Echinocythereis whatleyi*. In this region, therefore, the combination of narrow, but unstable, temperature and salinity ranges involved (3,18–3,25°C and 34,75–34,84‰ in the north, to 2,91–2,79°C and 34,68–34,73‰ in the south) afford a highly favourable ecological niche for at least three species to exploit opportunistically. At the same time, this zone separates AAIW—in which *H. melobesioides* is abundant and *Krithe* species relatively sparse, from NADW—in which the roles of these two taxa are almost reversed. However, neither of these species finds the conditions within the shear zone at all favourable. A further aspect of this complex response can be seen in the distribution of *H. melobesioides*, where the portion of the water mass in which it is most abundant (AAIW) has temperature and salinity characteristics of 2,9–3,3°C (mean 3,1°C) and 34,65–34,68‰ (mean 34,67‰), whereas the underlying water mass, which it finds so unfavourable, has characteristics of 2,78–3,1°C (mean 2,94°C) and 34,77–34,87‰ (mean 34,82‰). The differences involved are 0,16°C and 0,15‰, respectively, yet in the Neritic Zone (across the upper part of the SMZ) changes in temperature and salinity five times these values result in abundance changes only half as large.

## COMPARISON WITH RESULTS FROM OTHER AREAS

We will briefly review four recent studies on deep-water ostracod faunas in which attempts were made to correlate distribution with various environmental parameters, and then summarize the results in the light of our findings.

Cronin (1983) worked off the south-eastern USA but, because his survey did not assess environmental factors below 1 100 m, his data relate primarily to shallower depths than we have investigated. Nevertheless, there are similarities in faunal content that make comparison relevant. Cronin found that the two prime controls on depth ranges are the 15–8°C thermocline at 150 m, and the oxygen minimum zone (3 ml/l) between 200–800 m. These barriers define two main ostracod faunas: one within the O<sub>2</sub> minimum zone, and one below it. The latter includes some taxa similar to our bathyal faunas.

Benson *et al.* (1983) worked off the continental margin of north-eastern North America. They identified three ostracod faunas (biofacies), which they correlated with particular water masses. These faunas lie at 400–1 400 m (Labrador Sea Water mass; Upper Slope Biofacies); 1 500–2 399 m (North East Atlantic Deep Water mass; Transitional Biofacies); and >2 400 m (Denmark Strait Overflow Water mass; Lower Slope and Rise Biofacies). Benson *et al.* (1983) concluded that the limiting parameters are probably temperature, and possibly salinity. No correlation was observed between sediment type or the organic carbon content of sediments.

Rosenfeld & Bein (1978) worked off north-western Africa. Their study did not extend to abyssal depths but, as with Cronin's (1983) work, some similarity with our faunas makes comparison relevant. On the north-western African margin, there is a major faunal break on the upper slope that separates a 'shallow-water' (100–483 m) fauna from a 'deep-water' (470–2 859 m) fauna. Rosenfeld & Bein (1978) did not discuss the nature of the environmental parameters that maintain this boundary but assumed that it was temperature controlled (i.e. it marks the top of 'psychrosphere'). A northward elevation of this level was attributed to local upwelling. No linkage was detected between ostracod distribution and sediment texture.

Peypouquet & Benson (1980) compared the ostracod faunas from two traverses in the south-eastern Atlantic (off Walvis Bay, and off northern Angola). Their objective was to assess the role of the Walvis Ridge in limiting the distribution of various taxa. They identified three major depth-related faunas in the Angola Basin and two in the Cape Basin (no samples were collected below 3 000 m in the latter), and these were correlated with major water masses: epibathyal stage (400–1 500 m) = AAIW; mesobathyal stage (1 500–3 000 m) = NADW; and infrabathyal stage (3 700–4 700 m) = AABW. They detected differences in the epibathyal and mesobathyal faunas on either side of the Walvis Ridge, which they related to nutrient rich (particularly P and Si), Antarctic-derived water affecting higher bathymetric levels on the southern side of the ridge. It is the contrast in dissolved O<sub>2</sub> values, rather than minimal

variations in temperature and salinity, that is thought to maintain the faunal differences between the two basins.

Temperature, salinity, and dissolved oxygen are all cited as parameters that control the depth ranges of ostracod species, as well as regulating population abundances and diversity. However, the four previous surveys that we have reviewed, as well as our own results, illustrate that their roles vary from species to species, and also vary for a given species within the water column. Peypouquet & Benson (1980) also suggested that variations in nutrient levels and dissolved oxygen can be responsible for major lateral taxonomic differences on a regional scale. As barriers to vertical distribution, local high gradients in any of the parameters we have mentioned can be expected to be limiting, and this is particularly the case in relatively shallow water. Consequently, the shelf/slope thermocline (e.g. Cronin's 1983 data), and shelf oxygen minima (e.g. eastern boundary upwelling systems, such as that off south-western Africa) can be expected to constitute major faunal barriers. In deeper water, lower gradients may not appear to have the same potential but nevertheless are equally effective. It follows, therefore, that the deep-water taxa are less tolerant of, say, temperature and salinity changes, or critical combinations thereof. The latter presumably must be the case for species, such as *Henryhowella melobesioides*, to cite a local example, that have a wide depth range. In fact, the concept of a 'depth range' is misleading because it merely reflects a range over which certain physico-chemical parameters are tolerable. As all the studies we have cited confirm, these tolerance ranges are governed by the characteristics of the ambient water masses. In the deep sea, therefore, the vertical faunal zonation merely reflects the local structure of the water column.

#### INTRA-OCEANIC RELATIONSHIPS

Table 12 shows the vertical distribution of key taxa from the deep-water studies in the Atlantic Ocean. Although certain taxa are universally present and often locally abundant, both in the lower neritic, bathyal and abyssal zones (in particular various species of *Henryhowella*, *Cytherella*, and *Krithe*), there are some regional contrasts, which can be related to differences in water-column structure.

#### UPPER BATHYAL FAUNAS

Here we include ostracod populations between depths of 900–1 500 m. At the lower level, faunal breaks have been recognized off north-eastern America and south-western Africa (Peypouquet & Benson 1980 recorded a faunal boundary at this depth off Angola, although they had no data between 650–2 000 m), and this depth coincides with the upper limit of the NADW mass, which in the south-eastern Atlantic is overlain by AAIW, and in the North Atlantic by the Labrador Sea Water mass.



TABLE 12  
Key to the Atlantic Ocean distribution of deep-water ostracod taxa.

Depth	SE North America	NE North America	NW Africa	Angola	SW Africa
0					
200	<i>Trachyleberis</i>		<i>Macrocypris</i>		
400	<i>Cytherella</i> -2		<i>Cytherella</i> -?	<i>Cytherella</i> -?	
600	<i>Macrocypris</i>		Others-20	<i>Krithe</i> -1	<i>Krithe</i> -2
800	<i>Krithe</i> -?		-----	Others-4	<i>Henryhowella</i>
1 000	<i>Henryhowella</i>			-----	<i>Buntonia</i>
1 200	Others-37				<i>Rugocythereis</i>
1 400	-----				<i>Echinocythereis</i>
1 600	<i>Macrocypris</i>	<i>Krithe</i> -1			-----
1 800	<i>Henryhowella</i>	<i>Cytherella</i> -1			<i>Cytherella</i> -1
2 000	<i>Krithe</i> -?	Others-9		no data	<i>Krithe</i> -3
2 200	<i>Cytherella</i>		<i>Henryhowella</i>		<i>Echinocythereis</i>
2 400	Others-23		<i>Krithe</i> -2		<i>Rugocythereis</i>
2 600	-----		<i>Echinocythereis</i>		<i>Buntonia</i>
			<i>Buntonia</i>		-----
			<i>Cytherella</i> -?	no data	<i>Henryhowella</i>
				-----	<i>Buntonia</i>
		<i>Krithe</i> -2			<i>Rugocythereis</i>
		<i>Cytherella</i> -1			<i>Krithe</i> -5
		<i>Trachyleberis</i>			-----
		Others-6			<i>Echinocythereis</i>
				<i>Krithe</i> -6	Others-5
				<i>Buntonia</i>	
				<i>Cytherella</i> -?	
				<i>Trachyleberis</i>	<i>Trachyleberis</i>
				<i>Henryhowella</i>	<i>Krithe</i> -7
				<i>Echinocythereis</i>	<i>Cytherella</i> -1
				<i>Rugocythereis</i>	<i>Dutoitella</i>
		<i>Krithe</i> -3			<i>Poseidonamicus</i>
		<i>Echinocythereis</i>			<i>Abyssocythere</i>

2 800	Henryhowella	.....	Macrocypis	Echinocythereis
	Trachyleberis	.....	Others-5	Rugocythereis
Abyssal	Rugocythereis	.....	-----	Henryhowella
3 000	Poseidonamicus	.....		.....
3 200	Cytherella-1		no data	
3 400	Macrocypis-1			
	Dutoitella			
3 600	Others-11			
	3 200.....			
4 000			Buntonia	no data
			Trachyleberis	
4 200			Henryhowella	
			Echinocythereis	
4 400			Poseidonamicus	
			Dutoitella	
4 600			Kritho-4	
			Macrocypis	.....
			Others-6	.....
4 800			.....	.....
			.....	.....

..... — limits of survey  
 ----- — faunal boundaries  
 ..... — limits of data set  
 -(n) — no. of species  
 Others — miscellaneous species

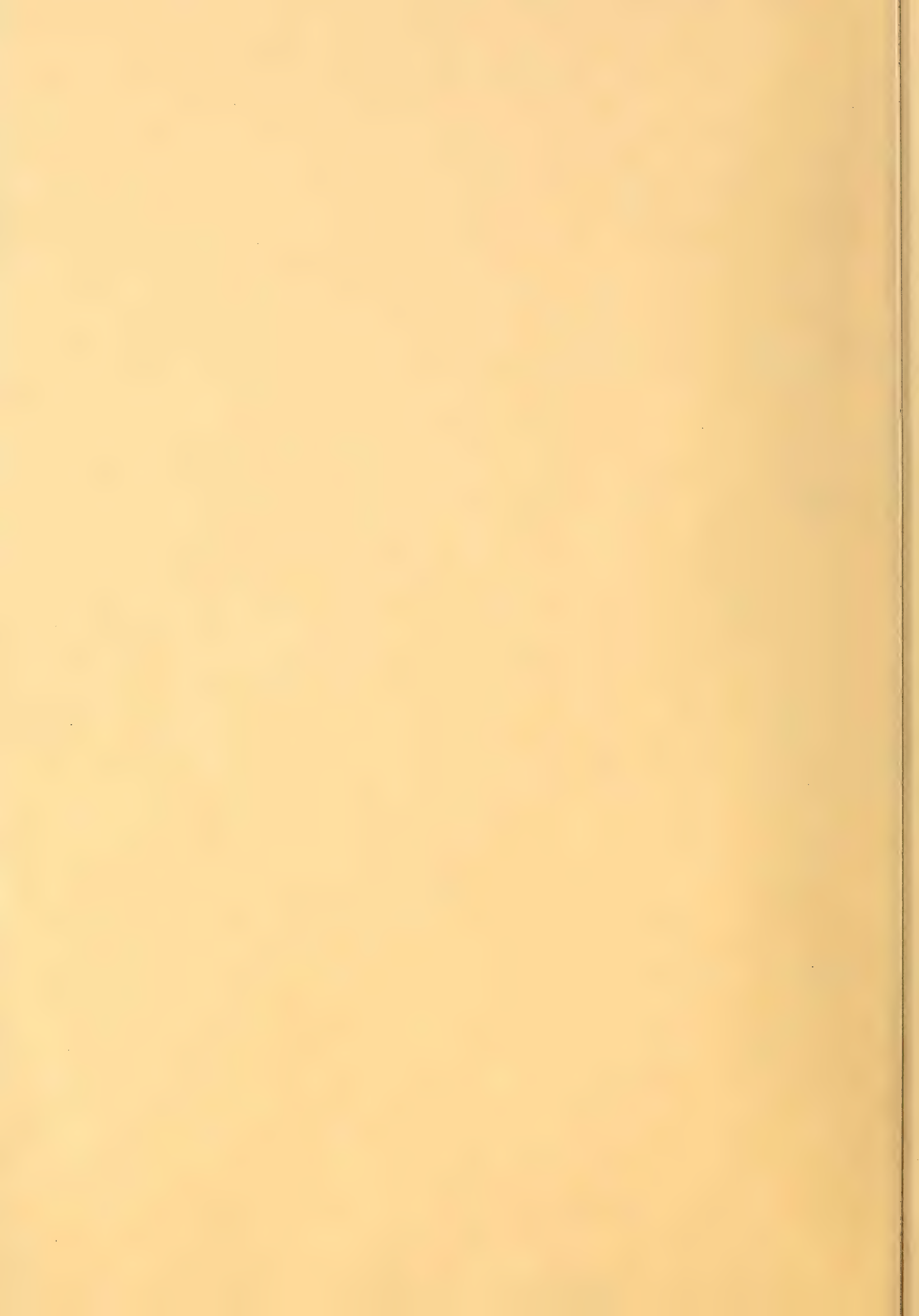




TABLE 12  
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	Depth	SE North America	NE North America	NW Africa	Angola	SW Africa
	0					
	200	<i>Trachyleberis</i>		<i>Macrocypris</i>		
		<i>Cytherella</i> -2		<i>Cytherella</i> -?		
	400	<i>Macrocypris</i>		<i>Others</i> -20	<i>Cytherella</i> -?	
		<i>Krithe</i> -?	-----		<i>Krithe</i> -1	<i>Krithe</i> -2
	600	<i>Henryhowella</i>		-----	<i>Others</i> -4	<i>Henryhowella</i>
		<i>Others</i> -37				<i>Buntonia</i>
	800	-----				<i>Rugocythereis</i>
		<i>Macrocypris</i>	<i>Krithe</i> -1			<i>Echinocythereis</i>
		<i>Henryhowella</i>	<i>Cytherella</i> -1			-----
	1 000	<i>Krithe</i> -?	<i>Others</i> -9		no data	<i>Cytherella</i> -1
Upper Bathyal	1 200	<i>Cytherella</i>				<i>Krithe</i> -3
		<i>Others</i> -23				<i>Echinocythereis</i>
	1 400	-----		<i>Henryhowella</i>		<i>Rugocythereis</i>
				<i>Krithe</i> -2		<i>Buntonia</i>
	1 600			<i>Echinocythereis</i>	-----	-----
Lower Bathyal	1 800			<i>Buntonia</i>		<i>Henryhowella</i>
				<i>Cytherella</i> -?		<i>Buntonia</i>
	2 000		<i>Krithe</i> -2		no data	<i>Rugocythereis</i>
			<i>Cytherella</i> -1			<i>Krithe</i> -5
	2 200		<i>Trachyleberis</i>			-----
			<i>Others</i> -6			
	2 400				<i>Krithe</i> -6	<i>Trachyleberis</i>
	2 600				<i>Buntonia</i>	<i>Krithe</i> -7
					<i>Cytherella</i> -?	<i>Cytherella</i> -1
					<i>Trachyleberis</i>	<i>Dutoitella</i>
					<i>Henryhowella</i>	<i>Poseidonamicus</i>
					<i>Echinocythereis</i>	<i>Abyssocythere</i>
					<i>Rugocythereis</i>	
	2 800		<i>Krithe</i> -3			
			<i>Echinocythereis</i>			
	3 000				<i>Macrocypris</i>	<i>Echinocythereis</i>
Abyssal			<i>Henryhowella</i>		<i>Others</i> -5	<i>Rugocythereis</i>
	3 200		<i>Trachyleberis</i>	-----		<i>Henryhowella</i>
			<i>Rugocythereis</i>			-----
	3 400		<i>Poseidonamicus</i>			
			<i>Cytherella</i> -1		no data	
	3 600		<i>Macrocypris</i> -1			
			<i>Dutoitella</i>			
	4 000		<i>Others</i> -11			
			3 200:-----		<i>Buntonia</i>	no data
	4 200				<i>Trachyleberis</i>	
					<i>Henryhowella</i>	
	4 400				<i>Echinocythereis</i>	
					<i>Poseidonamicus</i>	
	4 600				<i>Dutoitella</i>	
					<i>Krithe</i> -4	
	4 800				<i>Macrocypris</i>	
					<i>Others</i> -6	-----
					-----	-----

----- — limits of survey  
 ----- — faunal boundaries  
 ----- — limits of data set  
 -(n) — no. of species  
 Others — miscellaneous species

With the exception of north-eastern America (which has an atypical, low-diversity Arctic shelf fauna displaced on to the slope by the southwardly descending Labrador Sea Water), all the areas have a moderately diverse ostracod fauna that includes various species of the universal taxa (*Krithe*, *Cytherella*, *Henryhowella*, *Legitimocythere* (including '*Thalassocythere*' of Benson), and *Cytheropteron*), as well as numerous more localized species that reflect the adjacent neritic populations. The latter, as we have intimated earlier, are strongly influenced by local oceanographic and sedimentological regimes. Consequently, the upper bathyal faunas vary considerably on a regional scale, whilst retaining a large degree of similarity via their universal taxa. In particular, the abundance of *Henryhowella* and a relatively abundant and diverse component of *Krithe* (compared to the neritic faunas) are characteristic.

The Upper Bathyal fauna off south-western Africa differs from that at the other localities in one important respect, viz. the presence of *Rugocythereis* and *Echinocythereis whatleyi*, and the absence of *Macrocypris* and *Bythocypris*.

#### LOWER BATHYAL AND ABYSSAL FAUNAS

The depth of the faunal boundary between the abyssal and lower bathyal assemblages varies regionally, depending on the local structure of water column. In the Cape Basin, we find a faunal break at about 2 000 m marked by the appearance of *Poseidonamicus major* and the disappearance of *Buntonia rosenfeldi* and other species. However, because *Poseidonamicus* occurs on the continental shelf off south-western Africa, its presence may not be so significant in indicating abyssal assemblages as previously assumed, and that more typical abyssal faunas appear with *Abyssocythere*, *Dutoitella*, and *Krithe peypouqueti* at 2 916 m. This distribution, in fact, is very similar to that off north-eastern America, where Benson *et al.* (1983) found equivalent taxa appearing over similar depth ranges—*Poseidonamicus* somewhere between 1 500 m and 2 500 m, and *Dutoitella* (recorded as '*Suhmicythere*') at 3 000 m. These two areas differ from the Angola Basin, where *Poseidonamicus* does not occur above 3 000 m and *Dutoitella* (as '*Shumicythere*' [sic]) above 3 797 m (Peypouquet & Benson 1980). This is probably a result of structural differences in the water column between the Cape and Angola basins, where AABW is largely prevented from intruding into the latter by the Walvis Ridge. In fact, Peypouquet & Benson (1980) suggested that the Angola Basin has a North Atlantic aspect to its deep-water fauna (typified by the presence of *Pterygocythere mucronalatum* (Brady, 1880)), which is caused by the Walvis Ridge shielding the area from the nutrient-rich (particularly P and Si) Antarctic-derived waters. We are not convinced that this effect is significant above the 4 000 m level, because the regional gradients in both parameters do not seem anomalous either side of the ridge (see Gorschov 1978, figs 237D, 238A, 239C–D), and suspect that oceanic upwelling off south-western Africa may be a more important factor.

Rosenfeld & Bein (1978) sampled the margin off north-western Africa to a maximum depth of 2 859 m but did not record any of the typical abyssal taxa,

although both *Buntonia rosenfeldi* and *Echinocythereis whatleyi* occur at this depth. This indicates that the Lower Bathyal fauna extends to greater depths off north-western Africa than either in the north-western or south-eastern Atlantic regions, and it may be significant that the temperatures and salinities at this depth are higher off north-western than off south-western Africa: 2,75°C, 34,94‰, and 2,53°C, 34,89‰, respectively (Fuglister 1960).

In summary, the ostracod faunas off south-western Africa display a deep-water aspect, both in their bathyal and abyssal elements, at shallower depths than most of the more northerly sites that have previously been investigated. Specifically, *Rugocythereis* and *Echinocythereis whatleyi* both range into the lowermost Neritic Zone (i.e. above 950 m), *Bythocypris* and *Macrocypris* do not range into the Bathyal Zone, and—with the possible exception of north-eastern North America—*Poseidonamicus* (2 000 m) and *Dutoitella* and *Abyssocythere* (3 000 m) occur above their counterparts elsewhere. We attribute these differences to lower water temperatures and salinities caused by a combination of local oceanic upwelling (Benguela system), and the area's proximity to and ease of access for Antarctic water masses.

### CONCLUSIONS

Important changes in the vertical distribution of deep-water ostracods off south-western Africa occur at major physico-chemical boundaries between and within the main water masses (Table 13). The faunas between these boundaries have the following characteristics:

1. Between the base of the SMZ/bathyal thermocline and the AAIW/NADW boundary there is a cosmopolitan bathyal assemblage, numerically dominated by *Henryhowella melobesioides*, with a diverse *Krithe* species fauna, together with important *Cytherella serratula*, *Cytheropteron cronini*, *Echinocythereis whatleyi*, and *Rugocythereis horridus*.
2. Between the AAIW/NADW boundary and the top of the NADW core the assemblage is dominated by *Krithe* species, with *H. melobesioides* rapidly decreasing in numbers with increasing water depth.
3. An abyssal assemblage occurs below a level near the top of the NADW core (between 1 780 m and 2 070 m), which marks the upper depth limit of *Poseidonamicus major*.
4. At a level somewhere between 2 070 m and 2 916 m there is a further influx of abyssal taxa: e.g. *Dutoitella suhmi*, *Abyssocythere australis*, *Krithe peypouqueti*, *K. rex*, and *Trachyleberis* sp. 3017 (= *Legitimocythere*).
5. The AABW assemblage consists of sparse, poorly preserved *Krithe* sp. and *Legitimocythere*.

Our data suggest that migration of taxa up- and down-slope is regulated by physico-chemical changes in the water column acting as barriers or filters. These have the effect of maintaining the integrity of the assemblages of the intervening sectors of the water masses.



TABLE 13  
Summary of species distribution in faunal zones and water masses.

Fauna	Upper Bathyal	Lower Bathyal	Abyssal		
Depth (km)	0,95	1,5	2,0	3,0	4,0
Water masses	AAIW	N A D W core			AABW
<i>Trachyleberis</i> sp. 3017			x		x
<i>Krithe peypouqueti</i>			x		x
<i>Krithe rex</i>			x		
<i>Cytherella</i> sp. 3027			x		
<i>Krithe</i> sp. 22			x		
<i>Dutoitella suhmi</i>			x		
<i>Abyssocythere australis</i>			x	n	
<i>Poseidonamicus major</i>			x	o	
<i>Ambocythere</i> sp. 3057			x		
<i>Cytheropteron</i> sp. 2914			x	s	
<i>Krithe</i> sp. 6		x	x	a	
<i>Krithe</i> sp. 19		x	x	m	
<i>Krithe</i> sp. 7		x	x	p	
<i>Krithe</i> sp. 4		x	x	l	
<i>Cytherella serratula</i>	x	x	x	e	
<i>Cytheropteron cronini</i>	x		x	s	
<i>Echinocythereis whatleyi</i>	x	x	x		
<i>Rugocythereis horridus</i>	x	x	x		
<i>Buntonia rosenfeldi</i>	x	x	x		
<i>Henryhowella melobesioides</i>	x	x	x		
<i>Krithe spatularis</i>	x	x			
Indet. sp. 23	x				
Indet. sp. 62	x				
<i>Parakrithe</i> sp. 10	x				
<i>Cytheropteron</i> sp. 2909	x				
<i>Krithe</i> sp. 8	x				
<i>Krithe capensis</i>	x				
<i>Buntonia</i> sp. 34*	x				
<i>Xestoleberis</i> sp. nov.*	x				
? <i>Bradleya</i> sp. 56*	x				
<i>Bythocypris</i> sp. 42*	x				

\* - neritic taxa

These observations lead to the important conclusion that the major water masses, and important structural features within them, can be characterized by their ostracod assemblages. This provides a potential tool for environmental and palaeo-oceanographic investigation, and Dingle *et al.* (1989) have presented a preliminary discussion of its application, based on our results from south-western Africa. Extension of this work, involving a comparison of the Cape Basin data with previous studies from other parts of the Atlantic, indicate that deep-water ostracod assemblages can be used to discriminate water masses

on an ocean-wide basis (Dingle & Lord in press.). This suggests that benthic ostracods can be employed in a similar manner to benthic foraminifera in palaeo-oceanographic studies, and an ostracod assemblage/water-mass correlation scheme, parallel to that achieved for foraminifera by, for example, Schnitker (1980) and Douglas & Woodroff (1981), is a foreseeable development.

Distribution and environmental studies in other oceans (e.g. Whatley & Ayress 1988; Hartmann & Hartmann-Schroder 1988; Steineck *et al.* 1988) should permit the application of a correlation scheme for deep-water ostracod assemblages and water masses world-wide. However, direct correlation between species and the complex relationships linking conservative (e.g. temperature and salinity) and non-conservative (e.g. dissolved oxygen and silica) water parameters will probably require considerably more effort, if the progress achieved in foraminiferal studies is a measure of the difficulties involved.

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- WHATLEY, R. C., HARLOW, C. J., DOWNING, S. E. & KESLER, K. J. 1983. Observations on the origin, evolution, dispersion and ecology of the genera *Poseidonamicus* Benson and *Bradleya* Hornibrook. In: MADDOCKS, R. L. ed. *Applications of Ostracoda. Proceedings 8th International Symposium on Ostracoda*, Houston, 1982: 492–509. Houston: Department of Geosciences, University of Houston.











6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierii* Philippi, 1861: 87.

*Leda bicuspidata*: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

*Holotype*

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

*Capital initial letters*

- The Figures, Maps and Tables of the paper when referred to in the text  
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives  
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Reference to the author should preferably be expressed in the third person

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Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



R. V. DINGLE, A. R. LORD

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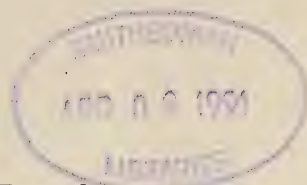
DEEP-WATER QUATERNARY OSTRACODA  
FROM THE CONTINENTAL MARGIN OFF  
SOUTH-WESTERN AFRICA  
(SE ATLANTIC OCEAN)

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# ANNALS

OF THE SOUTH AFRICAN  
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Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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- FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.
- FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.
- THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)



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A TOOTH-BEARING MAXILLA REFERABLE  
TO *LYCORHINUS ANGUSTIDENS* HAUGHTON,  
1924 (DINOSAURIA, ORNITHISCHIA)

By  
C. E. GOW

Cape Town

Kaapstad

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A TOOTH-BEARING MAXILLA REFERABLE TO  
*LYCORHINUS ANGUSTIDENS* HAUGHTON, 1924  
(DINOSAURIA, ORNITHISCHIA)

By

C. E. Gow

*Bernard Price Institute for Palaeontological Research, University  
of the Witwatersrand, Johannesburg, South Africa*

(With 7 figures)

[MS accepted 5 December 1989]

ABSTRACT

The taxonomic status of the genera *Lycorhinus* and *Heterodontosaurus*, and the various specimens referred to them, is in an unsatisfactory state, due to incomplete preparation and description of otherwise good material, a tendency to diagnose specimens rather than species, and a lack of understanding of the anatomy and functioning of the teeth. A new tooth-bearing maxilla is described in detail, and both it and the type and only specimen of *Lanasaurus scalpri-dens* Gow, 1975, are referred to *Lycorhinus angustidens* Haughton, 1924, which is also restudied and reinterpreted here. Although detailed descriptions of the dentition of *Hetero-dontosaurus tucki* Crompton & Charig, 1962, have not yet appeared, *L. angustidens* and *H. tucki* are readily distinguishable on postcanine tooth morphology, angle of wear facets, and pattern of occlusion. Authors have ranked these differently specialized contemporary species as primitive and advanced; this practice may be questioned.

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INTRODUCTION

In 1984 James Kitching and the author collected a tooth-bearing left maxilla of an Early Jurassic ornithischian dinosaur. Any new material of these rare and incompletely known animals is to be welcomed. As the specimen was studied it became apparent that it is a larger specimen of the species *Lanasaurus scalpri-dens* Gow, 1975, and that both are referable to *Lycorhinus angustidens* Haughton, 1924. Impressions were accordingly made of the type of *L. angusti-dens*, thus enabling a detailed study of the three specimens. The study shows that *Lycorhinus angustidens* differs from *Heterodontosaurus tucki* Crompton & Charig, 1962. Most described material resides comfortably in one or the other of



these species, with the exception of *Lycorhinus consors* Thulborn, 1974. The much discussed specimen UCL A100 (Thulborn 1970) was probably correctly identified as *L. angustidens*; it cannot be grouped with *L. consors* as *Abrictosaurus* Hopson, 1975. The intention of this paper is to refrain as far as possible from discussing the work of previous authors but rather to concentrate on presenting new facts and inferences.

The following abbreviations are used to indicate the repositories of the material studied:

- BP — Bernard Price Institute
- SAM — South African Museum
- UCL — University College, London.

## THE NEW MAXILLA

### *Locality*

The farm Bamboeskloof, Lady Grey: 30°45'S 27°12'E, map reference Floukraal 3027CC.

This locality is less than 15 km from two *Heterodontosaurus tucki* localities in the Herschel district (Crompton & Charig 1962; Santa Luca *et al.* 1976) and approximately 130 km from the type locality (Mount Fletcher) of *Lycorhinus angustidens* Haughton, 1924. *Lanasaurus scalpridens* Gow, 1975, was found about 250 km to the north (Golden Gate Highlands National Park). (See outcrop and locality map in Kitching & Raath 1984, fig. 1.)

### *Material*

The specimen (BP/1/5253) had been exposed to the elements for some time prior to collection, with the result that the more delicate dorsal and anterior projections of the maxilla are missing. The cutting edges of the teeth are also damaged and two crowns are missing.

### *Preparation*

Only a little mechanical preparation was necessary. This was followed by treatment with thioglycolic acid, but this was discontinued as some damage to the specimen became evident; this was in any case only cosmetic preparation. Useful X-ray plates were made from the specimen.

### *Description* (Figs 1, 3–5)

In occlusal view (Fig. 5) three important features are seen: the pit for reception of the lower canine, the deep cheek region, and the pronounced curvature of the dental arcade. The dentition is fully developed and well worn, indicating that this was a mature individual. There are 14 functional teeth and a rudimentary 15th. The teeth invite several descriptive analogies; they are broadest linguolabially and closely packed like a row of kernels on a maize cob. (The

teeth of *Lanasaurus scalpridens* are broadest mesiodistally, but this difference can be attributed to age—compare Fig. 6.) Lingually and labially the crowns stand out from the roots (as evident in the photographs and indicated by dotted lines in Fig. 1). This swelling of the crowns is reciprocated by swellings of the roots at the mesial and distal 'gum lines' (for example see tooth 5). The final analogy is that the teeth have a symmetrical cold-chisel shape with a constant included angle of about  $75^\circ$  between wear facets and labial crown surfaces. (The narrower teeth of *L. scalpridens* have an included angle of  $45^\circ$ . Thus, although the angle is age dependent, it is worth stressing for comparison with *Heterodontosaurus* that the new maxilla belonged to a mature individual.) This included angle is a useful means of comparison as it is not affected by damage to the cutting edge of the crown and it eliminates subjective reference to vertical and horizontal axes.

More anterior teeth have taller crowns, whereas mesiodistal crown width increases towards the back of the tooth row. The crowns have mesial and distal ridges on their lingual and labial surfaces separated by grooves from the main body of the crown; the distal ridges and grooves are more pronounced; on the lingual surface grooves persist for some time as wear proceeds and are thus important for assessing ages of teeth.

In the following text teeth are referred to by numerals for convenience. Part of a wear facet is preserved on 2 but this tooth and 3 have lost much of the crown tips; 5 is lightly worn with part of the posterior groove still present; 6 is younger than its neighbours, being very little worn; 7 appears to have complex wear, but the two small basal facets were probably induced by trapped food rather than direct tooth on tooth contact (this is an old tooth); 8 is also well worn. Here one begins to see the pattern that persists from this point posteriorly, whereby adjacent wear facets on successive teeth were formed by a lower tooth in staggered occlusion. This pattern becomes very clear when the teeth are viewed normal to the wear facets (Fig. 1B—lines on the left in the figure separate inferred lower teeth). Steps between adjacent teeth in this occlusal view immediately show up young teeth and correlate with those teeth (in Fig. 1C) that retain traces of a posterior groove (notably 6 and 9; 12 is more worn). Tooth 9 is lightly worn, 10 is heavily worn with some blurring between the two main facets, possibly the result of polishing by food but also possibly the remnant of an earlier facet (as argued for *Lycorhinus angustidens*—see below). Tooth 11 has a well-developed pair of wear facets. Tooth 12, though a moderately young tooth (presence of posterior groove), is complicated, as its anterior facet is actually paired—the result of being opposed by two successive lower teeth. This tooth also has a large food polish facet. Teeth 13 and 14 are well worn (retention of the posterior groove on the latter possibly due to delayed eruption of a suitable antagonist). The rudimentary tooth 15 indicates that this is a fully elaborated, mature dentition.

Teeth 6, 9 and 12 form a series of increasing age and are clearly younger than the two teeth that follow each. Replacement thus proceeds from back to

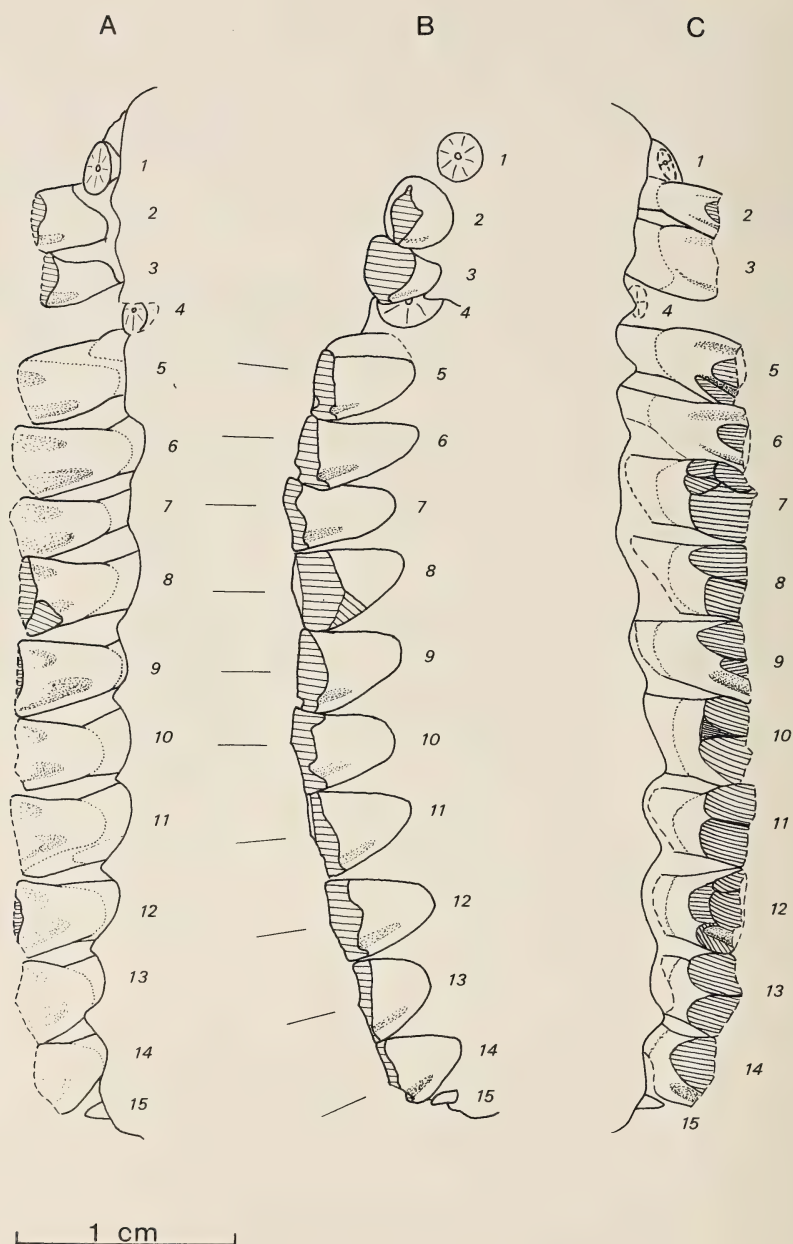


Fig. 1. *Lycorhinus angustidens*, BP/1/5253, left maxillary dentition. A. Labial view. B. Viewed normal to the wear facets. C. Lingual view. Note: In A and B hatching denotes broken areas. In C wear facets are hatched. Lines to the left of B indicated where lower teeth met each other.



front in the row. This is the same as the pattern described by Gow (1975) for *Lanasaurus scalpridens* (Fig. 6) and similar to that by Hopson (1975) for *Lycorhinus angusticeps* but with a slightly modified interpretation (see below).

This has interesting implications. In the described dentition, teeth within triplets are arranged in order of increasing age from front to back, but after two more replacements a stage would be reached when this order would be reversed, and it was just such a stage that pertained in the maxilla that opposed the type dentary of *Lycorhinus*, as demonstrated below. X-rays of the specimen reveal root canals filled with dense haematite; these show that only a very thin layer of maxillary bone roofs the deep tooth sockets: the canal fillings terminate at the alveolar border. In the tooth sequence 6 to 13, root-canal fillings are present for all except tooth 7—this is probably a quirk of preservation as 7 should be the last in the series 13–10–7 to be replaced. X-rays of *L. scalpridens* reveal a full complement of roots. Although these X-rays show no signs of replacement activity, this is not a firm indication that replacement had ceased. X-raying is a non-destructive technique that should be routinely applied and improved.

*Lycorhinus angustidens*

Figs 2, 3, 7

The specimen, SAM-3606, has been well described by Hopson (1975, 1980) but was re-examined for this study owing to the possibility (now considered confirmed) that the new maxilla belongs to the same species. In order to take impressions, the specimen was thoroughly wet and the excess water removed with compressed air; a fabric-reinforced latex impression was then made, the first layer being of a very watery consistency. Three impressions were taken and all are equally good. The impressions were coated with a fine film of sublimating ammonium chloride, and it is these that were studied and photographed.

The present interpretation differs slightly but significantly from that of Hopson (1980). The first point, which has not been stressed previously, is the marked curvature of the postcanine tooth row. When the canine is oriented with its cutting edges in a sagittal plane, the postcanine row curves back strongly labiad. (The new maxilla matches this curvature. The best way to see this is to orientate the photographs of the occlusal view with the first three teeth in the sagittal plane.)

The canine bears serrations on both edges (four per millimetre) as illustrated by Hopson (1980, fig. 1). However, most of the distal edge of the tooth is missing.

Postcanine 1 bears a small mesial cusplet and above it the margin of the crown is damaged (i.e. there may have been other cusplets). The posterior half of the labial surface of the crown is damaged and this looks like wear, as the damaged area has a sharp but smooth enamel edge (the worn area is covered with matrix grains firmly adhering to the dentine surface).

Postcanine 2 has a worn occlusal edge to the crown; it also has a mesiolabial wear facet almost certainly formed when the erupted tooth made contact with

the opposing upper tooth that had earlier been responsible for making the facet on 1M—the first indication of a staggered pattern of occlusion of upper and lower cheek teeth, which is argued in detail later. The condition of the labio-distal surface of 2 is not clear due to adherent matrix, but it does seem confluent with the anterior facet on 3.

Postcanine 3 has a small distal cusplet high on the crown. There is some conchoidal fracture of the dentine at the tip of the crown but this does not mask two distinct wear facets dipping slightly away from each other. Tooth 4 is very similar though more worn and better preserved. Hopson's (1980) interpretation of tooth 5, i.e. one major wear facet and a small polished area, is accepted. Hopson interpreted tooth 6 in the same way but the larger lower facet is in fact in perfect contiguity with the anterior facet on tooth 7, thus demonstrating the presence of an upper tooth in overlapping occlusion with 6 and 7.

Postcanine 7 is an old tooth; its posterior wear facet bears a wide, deep, smoothly rounded groove. This groove must have been formed by a step between adjacent edges of occluding upper teeth at different stages of wear. A small facet is present on the mesial edge of 8. By tilting the specimen it is possible to see that this facet lies on the same arc as the distal facet on 7—these facets are thus attributable to the same upper tooth. The author is not convinced that there is sufficient evidence for the same situation pertaining between 8 and 9, but agrees with Hopson (1980) that it seems likely. The large wear facets on 8 and 9 have deliberately been left unhatched in Figure 2 because these teeth

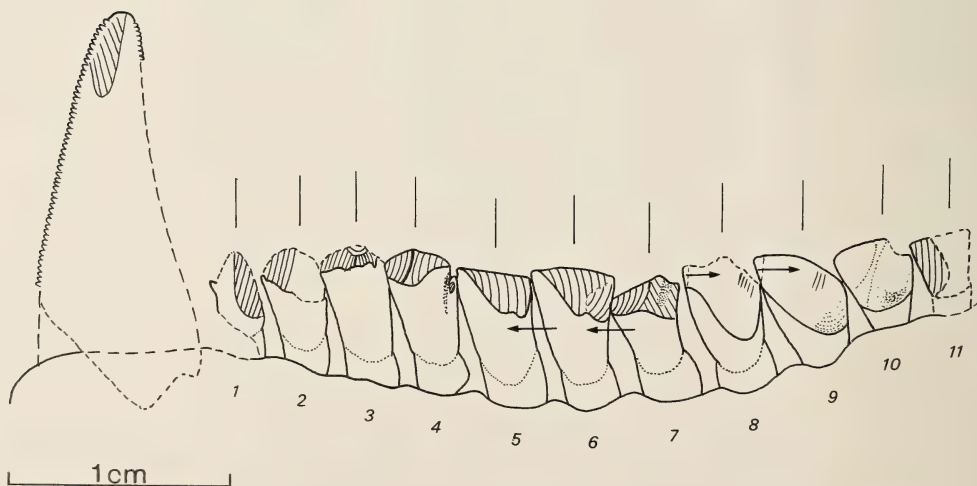


Fig. 2. *Lycorhinus angustidens*, SAM-3606. Impression of left dentary teeth. Hatching indicates wear facets but has been deliberately omitted from teeth 8, 9 and 10. Teeth 8 and 9 bear striations, 9 and 10 have heels shown by shading, and 10 bears a raised ridge with the same orientation as the striations on 8 and 9. Wear facet on canine is on the lingual surface of the tooth.

bear patches of striations indicating direction of bite. These striations are helpful to understanding the bite, which is seen to have a posteriad component. It is important to note that the striations have the same orientation as the ridge on tooth 10 discussed below. That such striations are rare suggests a degree of imprecision in the bite such that occluding surfaces are continuously roughly polished. Teeth 9 and 10 have heels worn into the base of their facets. The present interpretation of 10 and 11 differs from Hopson's but is made with the benefit of the hindsight afforded by the new maxilla. Tooth 10 has a raised ridge between facets, such as would result if the edges of occluding uppers did not quite meet.

The preserved portion of the 11th tooth was clearly part of a perfectly normal full-sized tooth; it is faceted and is raised labiad of 10, and it was thus opposed by the successor to the tooth responsible for the posterior facet on 10. It is suggested that the differences in wear facet orientation that Hopson (1980) recorded (supposedly increasingly horizontal with age) are illusory, as witness the continuity of facets on 7 with those of its neighbours. Indeed tooth 4 seemingly has the most nearly horizontal wear facets, but is less worn than tooth 5, which apparently has more oblique facets. This specimen represents a mature animal of a species characterized by very oblique wear facets. Three more teeth could have been present in the living dentary (see Fig. 3).

This dentition contains ample evidence of a staggered occlusal arrangement between upper and lower teeth. In Figure 2 vertical lines above teeth indicate where upper teeth would meet each other. Some of the most interesting and instructive lower teeth are those that at first sight apparently do not conform to this staggered pattern. The best place to begin is with tooth 6: here it is seen that a second wear facet has started to encroach on a previously existing single facet—the new facet would continue to enlarge and migrate forward as indicated by the arrow. One can postulate that exactly the same thing would happen in time to tooth 5. Teeth 8 and 9 differ in that they have very well-developed

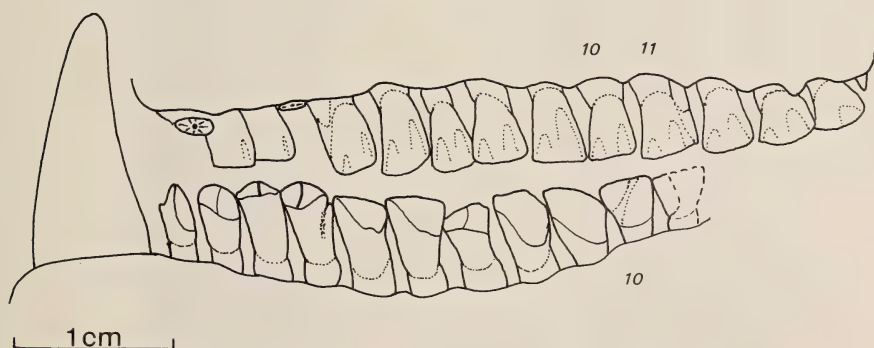


Fig. 3. *Lycorhinus angustidens*. Composite drawing of BP/1/5253 and SAM-3606. The specimens fit rather well and give an indication of the degree of incompleteness of the dentary tooth row. For reasons explained in the text, wear facets cannot be directly compared.



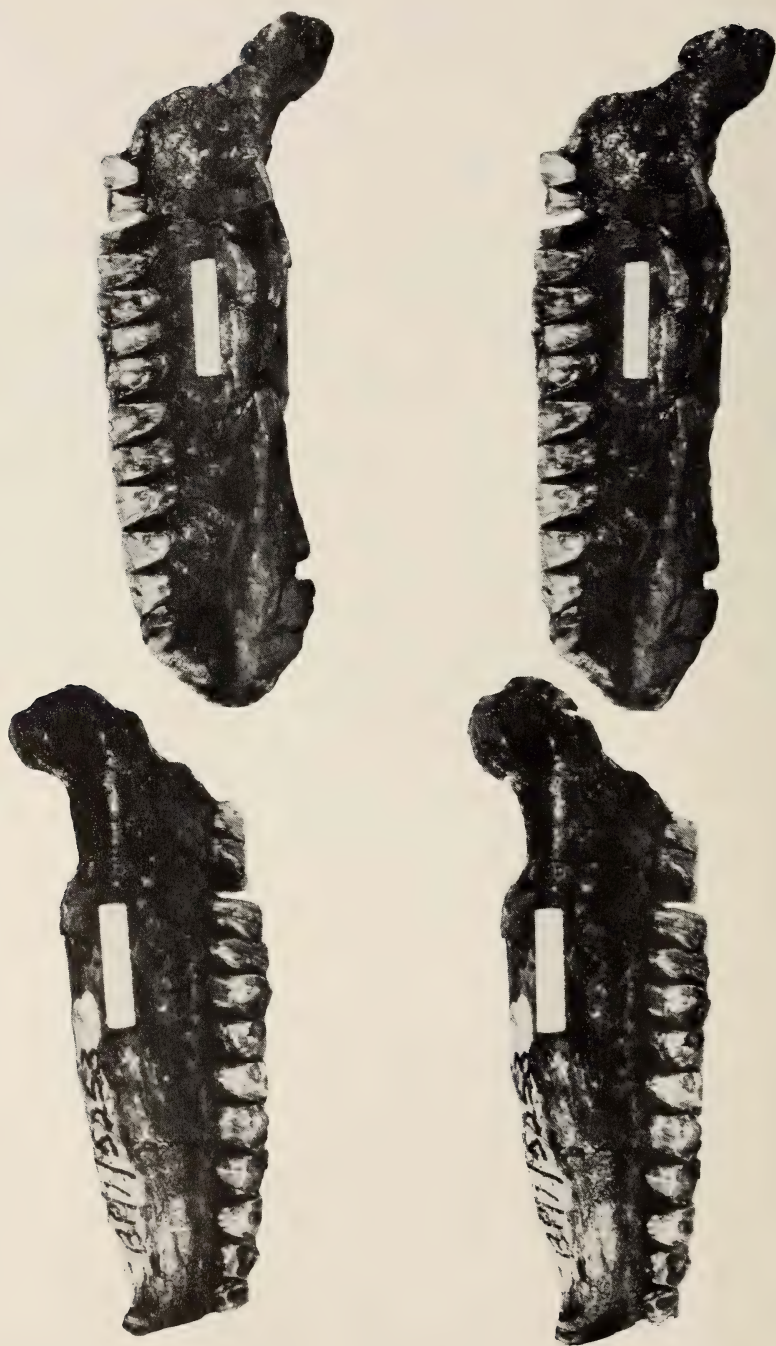


Fig. 4. *Lycorhinus angustidens*, BP/1/5253. Above. Labial view. Below. Lingual view.  
Scale bar = 1 cm.



Fig. 5. *Lycorhinus angustidens*, BP/1/5253. Above. Occlusal view. Below. View normal to wear facets. Scale bar = 1 cm.

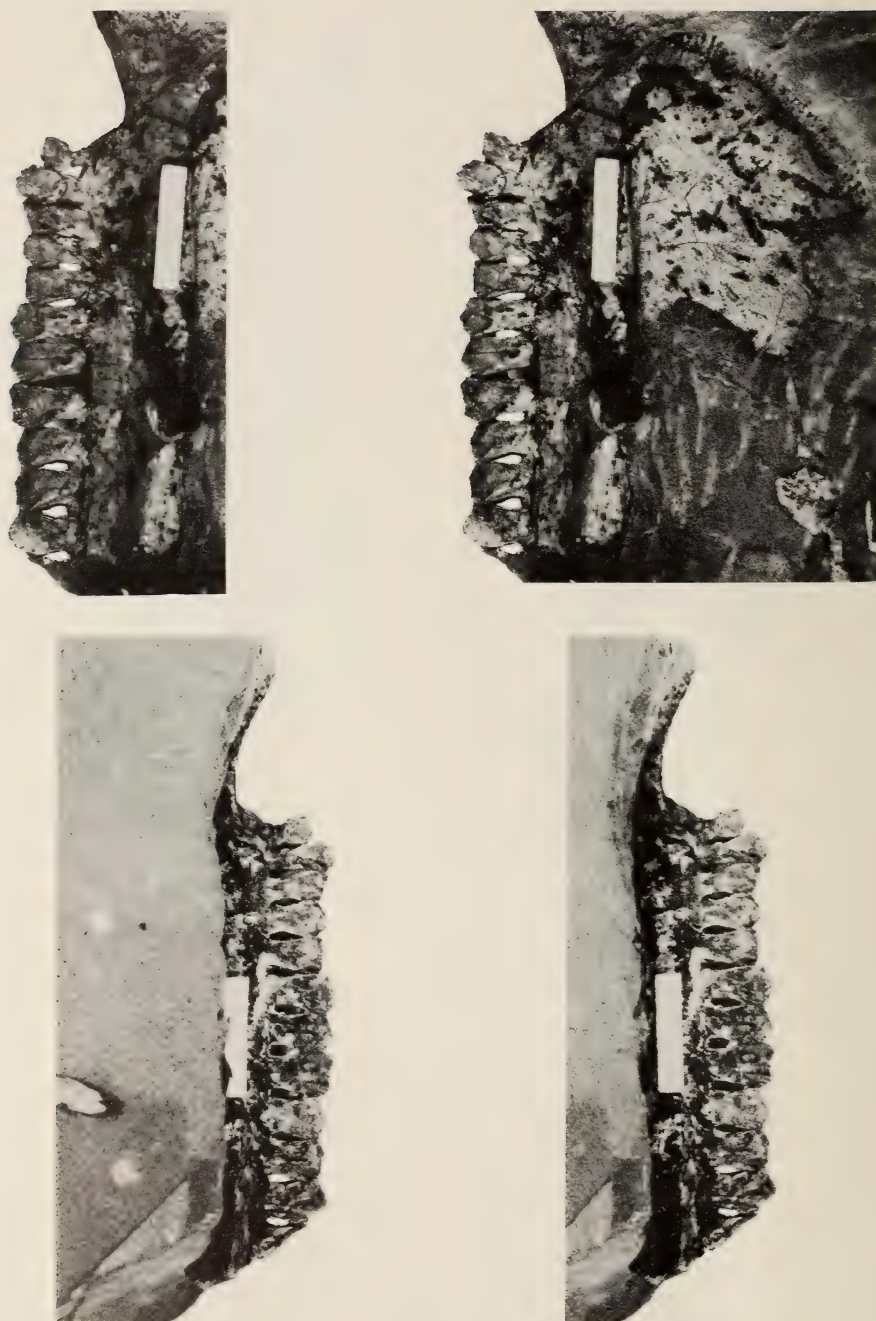


Fig. 6. *Lycorhinus angustidens* (*Lanasaurus scalpridens*), BP/1/4244. Above. Labial view. Below. Lingual view. Scale bar = 1 cm.



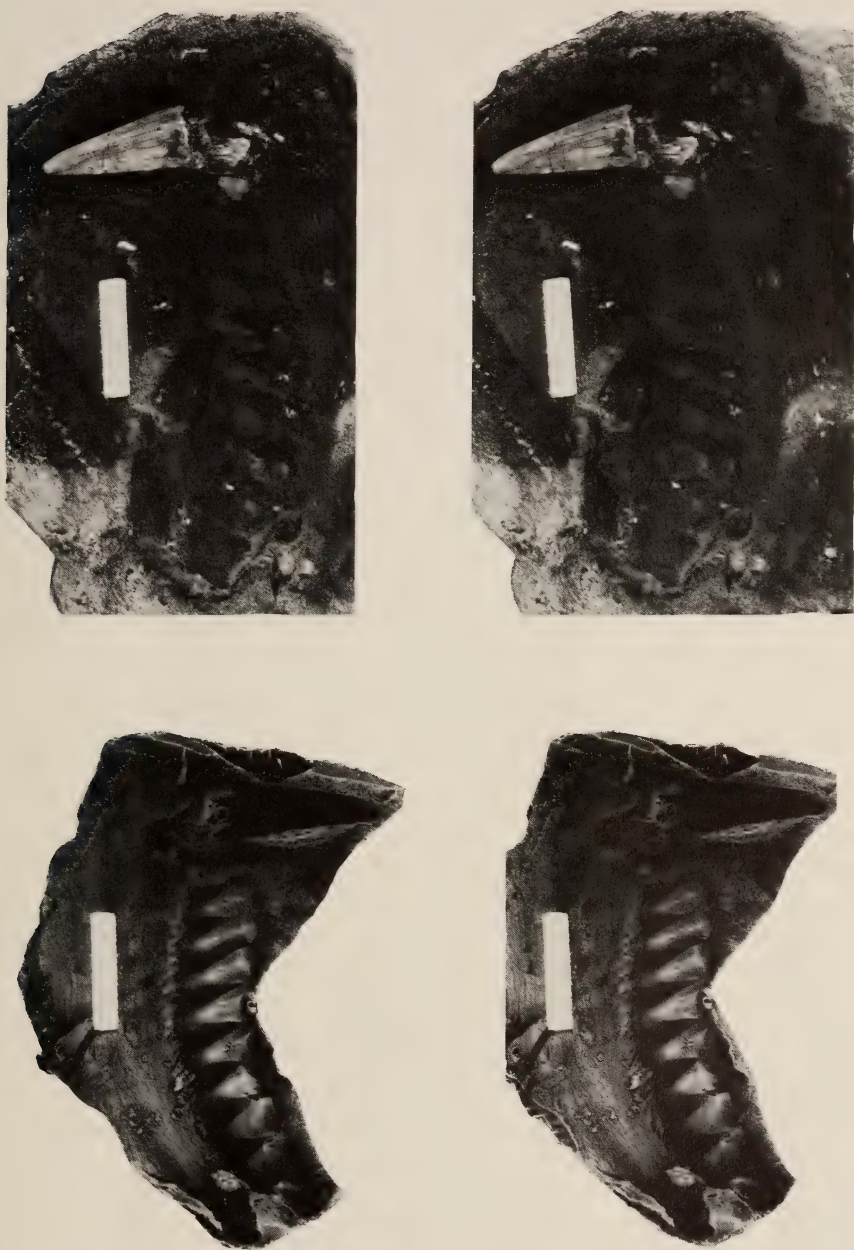


Fig. 7. *Lycorhinus angustidens*, SAM-3606. Original above. Positive impression below.  
Scale bar = 1 cm.

single facets, and incipient facets on their anterior edges. These latter facets would migrate posteriad in time until these teeth reached the condition seen in tooth 10, which has two distinct but very well-worn facets. After this the tooth would be shed. The difference in direction of facet migration has little to do with position in the tooth row, but seems rather to be related to the extent of wear of the teeth. From the above, the following sequence can be inferred.

(a) A single wear facet forms fairly symmetrically over the labial surface of the crown of a dentary tooth (as previously noted by Hopson such a facet is concave—the opposing upper teeth would be well worn and would present a convex surface). This is not apparent from Figure 1B and perceptions of facet curves change as the specimen is rotated about its longitudinal axis. At its best development each of a pair of facets on adjacent teeth is concave, hence a convexity is formed where they meet. This is seen in the occlusal stereophotograph (Fig. 5) between teeth 7 and 8, and 10 and 11.

(b) A second facet forms posteriorly when a new upper tooth comes into occlusion. This facet migrates forward and eventually dominates the crown as the tooth anterior to it is shed (this facet extends further down the crown—quite obviously this must be so).

(c) As a new tooth comes into occlusion in the anterior position, a third facet forms, this time on the anterior edge of the tooth, and this migrates backwards to result in the condition seen on tooth 10. At this stage the tooth would be replaced.

This interpretation highlights, and is itself supported by, the pattern of triplets in the *Lycorhinus* jaw. Arranged from youngest to oldest, these are 5, 6 and 7, and 8, 9 and 10. This interpretation differs from that of Hopson (1975, 1980), who proposed the following triplets: 4, 5 and 6, and 7, 8 and 9. Turning to the anterior teeth, it appears that 4 is more worn than 3, but both have two facets, whereas 2 has a single (first wear stage) facet; thus these teeth conform to the pattern of triplets proposed here.

We now have the interesting situation where both maxilla and dentary bear triplets of teeth that consistently range in age from front to back. For the lower jaw one can demonstrate that each triplet would require to be opposed by a battery of teeth in which the reverse situation pertained. To do this we can look at the hypothetical maxillary (M) triplet 6, 7 and 8 that occluded with dentary (D) teeth 6, 7, 8 and 9 at the time the bearer of the *Lycorhinus* type died. Tooth M6 was well ground in, M7 had only recently made contact with D8, whereas M8 may just have made contact with D9. We can also look at D9, 10 and 11: the oldest tooth in the next maxillary series should be M9—that fits; M10 should be mature but not as old as M9 and again this is borne out by the wear facet on D11. All this makes eminently good sense, as, if occluding teeth were to erupt together, the amount of attrition would presumably be greater and the teeth would wear faster.

The pattern of wear on the teeth in the new maxilla has been frozen at a different stage in the cycle, which makes it look different and more difficult to

interpret. The teeth appear more regularly bifaceted. That the same sequence as demonstrated for the dentary still applies, is shown by the following teeth: 9 has first and second wear stage facets, 12 is unusual in that first, second and third stage facets are present, whereas 7 has a partially obliterated second wear stage facet and a well-developed third wear stage facet. (Polish facets on 7 and 12 are ignored.)

## DISCUSSION

As a result of the foregoing description and analysis, tooth morphology, function and replacement are well understood, and the variation inherent in the system must lead to the conclusion that there is a high probability that *Lanasaurus scalpridens* and the new maxilla BP/1/5253 belong to the species *Lycorhinus angustidens*. The much discussed but poorly known specimen UCL A100 (Thulborn 1970) may also belong to this species.

The very similar species *Heterodontosaurus tucki* is known from a complete skeleton (Santa Luca *et al.* 1976), a complete skull (Crompton & Charig 1962), and possibly an undescribed jaw fragment (Charig & Crompton 1974).

*Lycorhinus consors* Thulborn, 1974, is an enigma, apparently possessing the teeth and wear pattern of *Lycorhinus* and the occlusal pattern of *Heterodontosaurus*.

*Heterodontosaurus* has more strongly ridged teeth with more transverse wear facets, and occlusion is nearly if not entirely opposite. Hopson (1980) demonstrated the same pattern of replacing triplets for *Heterodontosaurus*, as is now well documented for *Lycorhinus*.

Hopson (1980) remarked that the *Lanasaurus* maxilla was larger than the maxilla of *Heterodontosaurus*. The new maxilla is still larger, and fits the *Lycorhinus* dentary rather well; thus *Lycorhinus* could well have been a larger animal than *Heterodontosaurus*.

On the basis of the foregoing discussion, the maxilla BP/1/5253 is referred to *Lycorhinus angustidens* Haughton, 1924, and a revised synonymy for this species is presented below.

### *Lycorhinus angustidens* Haughton, 1924

*Lycorhinus angustidens* Haughton, 1924: 343–344, fig. 8. Thulborn, 1970: 236–241, figs 1–5.

*Abriotosaurus consors* (Thulborn, 1974) Hopson, 1975: 304 (part.—UCL A100 only).

*Lanasaurus scalpridens* Gow, 1975: 336–339, text-figs 1–2, pl. 1.

## ACKNOWLEDGEMENTS

I wish to thank the Director of the South African Museum, Dr M. A. Cluver, for the loan of the *Lycorhinus* type, Dr J. van den Heever who packed it so beautifully and Mrs Ann Lawton who kindly added the package to her family holiday luggage.



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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierti* Philippi, 1861: 87.

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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C. E. GOW

A TOOTH-BEARING MAXILLA  
REFERABLE TO  
*LYCORHINUS ANGUSTIDENS*  
HAUGHTON, 1924  
(DINOSAURIA, ORNITHISCHIA)



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A REVISED DESCRIPTION OF THE SKULL OF  
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By  
J. F. DURAND

Cape Town                      Kaapstad



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# A REVISED DESCRIPTION OF THE SKULL OF *MOSCHORHINUS* (THERAPSIDA, THEROCEPHALIA)

By

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*Bernard Price Institute for Palaeontology, University of the Witwatersrand\**

(With 17 figures)

[Paper presented at the Palaeontological Society of southern Africa Symposium, Cape Town, September 1986]

## ABSTRACT

Certain aspects of the external morphology of the *Moschorhinus* skull have been misinterpreted or overlooked in previous studies. In this paper the external morphology of the posterior half of the *Moschorhinus* skull is discussed in detail. The bony elements forming the braincase and the morphology of the foramina, fossae and grooves visible on the exterior surface of the braincase are described, and their possible functions are discussed. Certain misconceptions concerning the morphology of the prootic, opisthotic, quadrate, pterygoid, squamosal and epipterygoid are corrected. In the light of these findings the taxonomic position of *Moschorhinus* relative to other therocephalians is discussed.

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## INTRODUCTION

The interrelationships of the Therocephalia and their relationship with the Cynodontia are not adequately known. Certain authors, such as Broom (1938), Brink (1951), Hopson & Crompton (1969), and Kemp (1982), are of the opinion that the cynodonts had a therocephalian ancestor, whereas others such as Romer (1969) and Kermack & Kermack (1984) have argued that the cynodonts arose independently of the Therocephalia, from a more primitive ancestor. Most of the former authors accepted scaloposaur ancestry for the cynodonts, whereas Kemp (1972, 1982) argued that the cynodont ancestor was closely related to the whaitsiids.

To unravel therapsid phylogeny it is essential to know more about therocephalian morphology. The present study attempts to broaden our knowledge of

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*Moschorhinus kitchingi*, which is an interesting therocephalian with a mixture of primitive and advanced characteristics.

*Moschorhinus* seems to be more advanced than the pristerognathids and scaloposaurids, even though it has certain features in common with the gorgonopsians. *Moschorhinus* shares more characteristics with the whaitsiids than with any other therocephalian group. *Moschorhinus* is also more primitive than the whaitsiids but does not seem to be ancestral to them. The taxonomic position of *Moschorhinus* will be discussed in detail later.

The skull of *Moschorhinus* has been described by Broom (1920), Boonstra (1934), Brink (1959), and Mendrez (1974a). The elements forming the anterior half of the skull are well known from these descriptions. However, due to the poorly preserved braincase in most *Moschorhinus* specimens, or insufficient preparation thereof, certain misconceptions arose concerning the relations of the elements constituting the posterior half of the skull.

Two *Moschorhinus* skulls were selected for this study. Although these skulls are somewhat damaged and distorted, the posterior parts of the skulls are in such a condition that, with careful preparation it was possible to discover a wealth of information that adds to our knowledge of the *Moschorhinus* skull. In this paper the elements constituting the posterior half of the skull and the inter-relationships between these elements are described, and the possible courses of certain blood-vessels and nerves are discussed.

#### MATERIAL AND METHODS

Two previously undescribed specimens were selected for this study: *Moschorhinus kitchingi* (Broom) BP/1/2788 and BP/1/4636. BP/1/2788 was found by J. W. Kitching in Stoffelton, Afdeel Native Trust (now part of KwaZulu), near Bulwer, Natal, in the *Daptocephalus* zone (Kitching 1977) (*Dicynodon lacerticeps*-*Waitsia* Assemblage-zone—S.A.C.S. 1980). BP/1/4636 was found by J. W. Kitching on the farm Fairydale in the Bethulie district, Orange Free State in the *Lystrosaurus* zone (Kitching 1977) (*Lystrosaurus*-*Thrinaxodon* Assemblage-zone—S.A.C.S. 1980).

##### *Moschorhinus kitchingi*, BP/1/2788 (Figs 1–4)

Most of the matrix surrounding this skull had been removed with a hammer and chisel prior to this study. The matrix within the temporal cavities had not been removed. This distorted specimen is 21,5 cm long. The major parts of the skull roof and occiput are missing and the jugal and postorbital arches are damaged. Teeth are present in the damaged and distorted mandible. Aspects of this specimen's teeth and mandible were used in the reconstruction of the lateral view of the skull (Fig. 14).

##### *Moschorhinus kitchingi*, BP/1/4636 (Figs 5–11)

The whole skull was prepared for this study by means of an air-hammer and engraving tool. This distorted skull is 25 cm long. Parts of its jugal and post-



orbital arches are missing and the occiput is damaged. Although this skull is severely damaged, it yielded vital information. The descriptions and reconstruction of the posterior part of the skull and the dental formula are those of this specimen (Figs 12–17).

### DESCRIPTION

The posterior half of the *Moschorhinus* skull consists of the following endochondral elements: the epipterygoid, prootic, opisthotic, quadrate, supraoccipital, exoccipital and basioccipital, and the following dermal elements: the squamosal, quadratojugal, jugal, interparietal, parietal, postorbital, tabular and pterygoid. The parasphenoid and basisphenoid are of endochondral and dermal origin.

The lateral wall of the braincase can be seen within the jugal arch (Fig. 16). The large parietal forms the sharp-crested roof of the braincase and the dorsal border of the temporal fossa. The posterior wall of the temporal fossa is largely formed by the squamosal. The medial wall of the temporal fossa is formed by the epipterygoid, the prootic, the ventrolateral part of the pterygoid, the lateral part of the opisthotic, and anterior parts of the supraoccipital and interparietal. Several features relating to blood-vessels and nerves can be seen within the temporal fossa.

The posterior surfaces of the parietal, interparietal and supraoccipital form the medial surface of the occiput, dorsal to the foramen magnum (Fig. 15). These elements are flanked by the tabulars, which cover part of the squamosal posteriorly. The lateral part of the occiput is formed by the posterior parts of the squamosal and the opisthotic. The foramen magnum is flanked by the exoccipitals. The ventromedial border of the occiput is marked by the basioccipital. Two of the most salient features of the occiput are the large post-temporal fenestra and the paroccipital fossa.

#### EPIPTERYGOID (Figs 12–14, 16)

In lateral view (Figs 14, 16), the flattened, blade-like epipterygoid can be seen. It contacts the parietal, supraoccipital and prootic dorsally and the pterygoid, prootic and squamosal ventrally. The upper part of the processus ascendens (dorsal lamina—Mendrez 1972, 1974a, 1974b) expands anteriorly to form an anterodorsal process and posteriorly to form a posterodorsal process. The basal part of the epipterygoid expands anteriorly to form an anteroventral process and posteriorly to form a posteroventral process (Mendrez 1972, 1974a, 1974b). A small posterior apophysis is present on the posterior edge of the processus ascendens, which probably made contact with the lateral part of the base of the anterodorsal process of the prootic (unfortunately damaged in all *Moschorhinus* specimens examined). The ventromedial part of the posterodorsal process of the epipterygoid contacts the anterolateral part of the anterodorsal process of the prootic just above the contact of the posterior apophysis with the prootic,



Fig. 1. *Moschorhinus kitchingi*. BP/1/2788. Dorsal view.



Fig. 2. *Moschorhinus kitchingi*. BP/1/2788. Ventral view.



Fig. 3. *Moschorhinus kitchingi*. BP/1/2788. Lateral view.

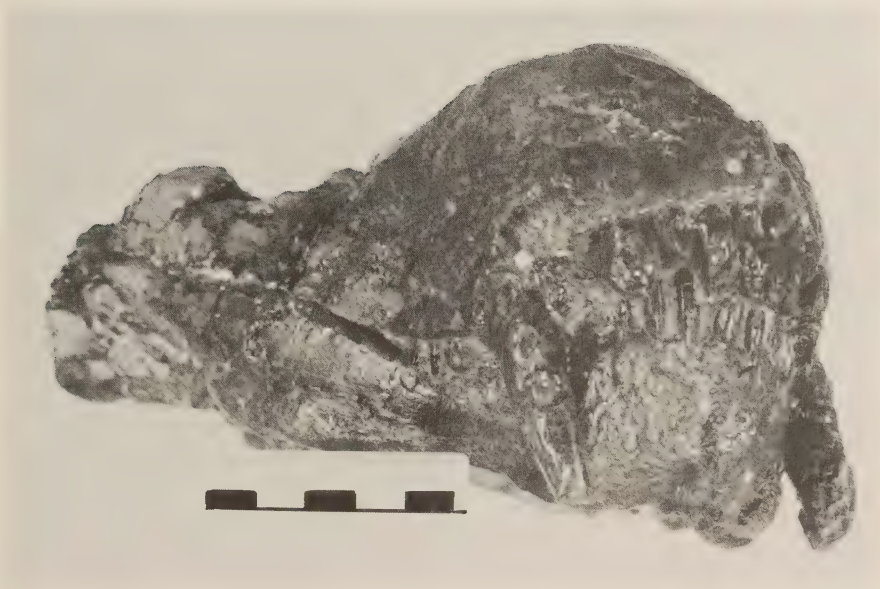


Fig. 4. *Moschorhinus kitchingi*. BP/1/2788. Oblique anterior view.



thus forming a circular foramen—the posterior foramen of the epipterygoid ('foramen veineux'—Mendrez 1974a) (see Fig. 16). There is a shallow funnel-like indentation surrounding the foramen on the lateral surface of the epipterygoid. A low ridge runs diagonally across the lateral surface of the epipterygoid from the tip of the posterodorsal process, passes anterior to the foramen, and terminates in the middle of the ventral part of the epipterygoid as a small tuberosity. This posterior foramen of the epipterygoid should not be confused with the dorsal venous foramen (see discussion). The dorsal border of the epipterygoid fits in snugly under the parietal. The central part of the dorsal border of the epipterygoid is overlapped laterally by the ventrolateral descending flange of the parietal. The tip of the posterodorsal process curves slightly downwards, away from the parietal, exposing the interparietal upon which the dorsal part of the posterodorsal process lies.

The anteroventral process of the epipterygoid is quite small in relation to the posteroventral process. It originates anteroventrally from the base of the processus ascendens. The anteroventral process terminates anteriorly to the dorsolateral ridge of the pterygoid and is in confluence with the posterior corner of this ridge. The term anteroventral process of the epipterygoid is preferred to the 'pterygoid process of the epipterygoid' (Crompton 1955) since the whole of the ventral border of the epipterygoid contacts the pterygoid. The foot of the epipterygoid covers the dorsal surface of the anterolateral third of the quadrate ramus of the pterygoid (see Figs 12, 16).

The posteroventral process of the epipterygoid originates at the base of the processus ascendens from where it flares out posterolaterally as an elongated, horizontal fan, overlying the middle third of the quadrate ramus of the pterygoid. These two processes are confluent laterally and posteriorly but not medially and anteriorly. The posteroventral process is slightly raised medially along its whole length, producing a medially facing groove that originates under the vertically inclined anterior part of the posteroventral process. The groove tapers off as it approaches the posterior border of the posteroventral process. The term posteroventral process of the epipterygoid is preferred to the 'quadrate process of the epipterygoid' (Crompton 1955), since it is doubtful whether the epipterygoid actually did contact the quadrate in *Moschorhinus*.

The posterior part of the posteroventral process of the epipterygoid is fan-shaped. The lateral half of the posterior border stretches across the dorsal surface of the quadrate ramus of the pterygoid. The posterior border contacts the anterior border of the anteroventral process of the squamosal medially, the contact being visible in dorsal and ventral views. This region of the epipterygoid forms part of the anterolateral corner of the pterygo-paroccipital foramen (see Figs 12, 13, 16).

In lateral view (Fig. 16), the ventral suture of the epipterygoid runs in the middle of the lateral side of the structure formed with the quadrate ramus of the pterygoid. The suture dips anteriorly and then curves upwards delimiting the border of the anteroventral process. Posteriorly the suture runs diagonally

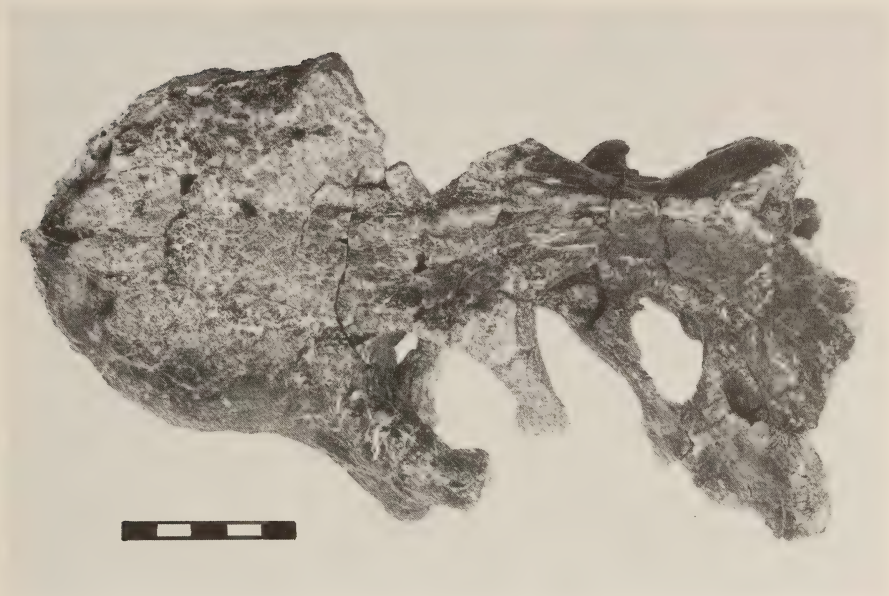


Fig. 5. *Moschorhinus kitchingi*. BP/1/4636. Dorsal view.



Fig. 6. *Moschorhinus kitchingi*. BP/1/4636. Ventral view.



upwards in a straight line delimiting the ventral border of the posteroventral process laterally on the dorsal side of the quadrate ramus of the pterygoid.

The processus ascendens of the epipterygoid juts upwards and slightly inwards. The middle part of the processus ascendens is relatively constricted in comparison with the dorsal and ventral parts, giving the epipterygoid an hour-glass shape in lateral view. The ventral part of the epipterygoid is directed outwards posteriorly and inwards anteriorly. This closely reflects the orientation of the quadrate ramus of the pterygoid, whereas the dorsal part of the epipterygoid is more parasagittally inclined.

A very distinct and large cavum epiptericum is present, bordered medially by the anteroventral process of the prootic and laterally by the epipterygoid. Certain nerves and veins traverse the cavum epiptericum (see discussion).

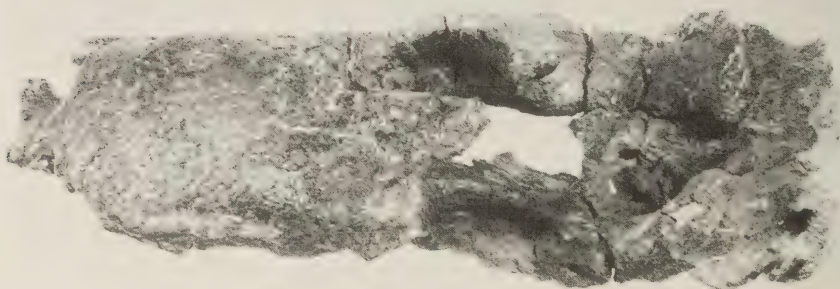


Fig. 7. *Moschorhinus kitchingi*. BP/1/4636. Left lateral view.

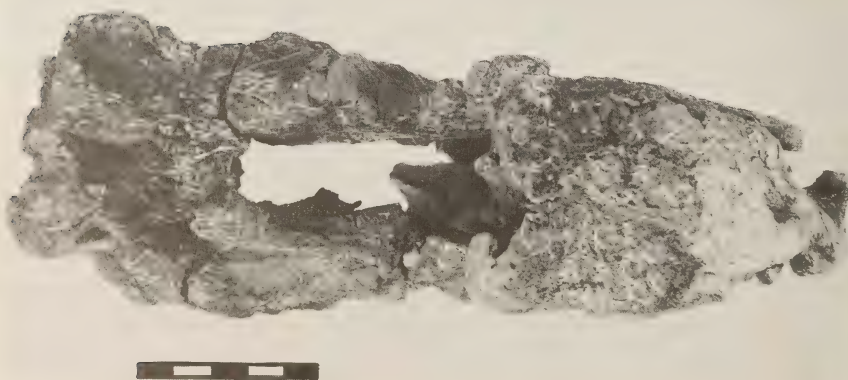


Fig. 8. *Moschorhinus kitchingi*. BP/1/4636. Right lateral view.



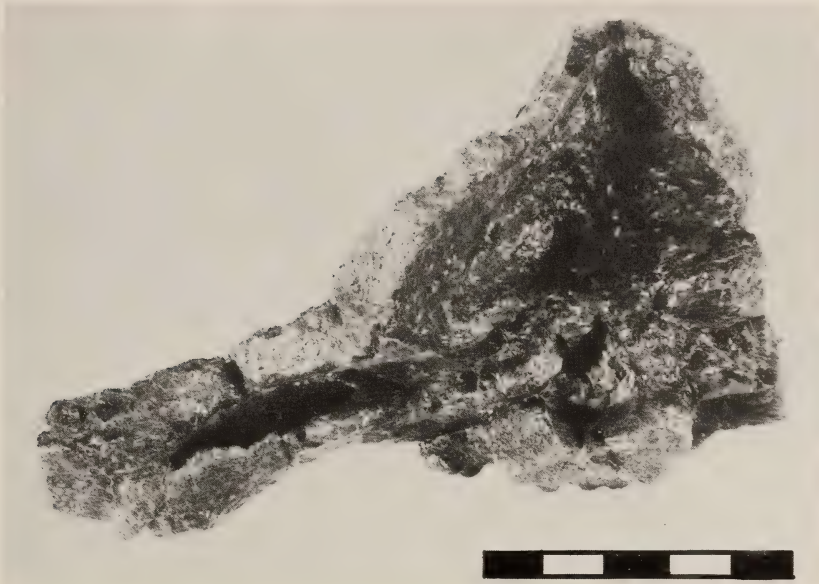


Fig. 9. *Moschorhinus kitchingi*. BP/1/4636. Occipital view.

#### PROOTIC (Figs 12–17)

The prootic and opisthotic are two separate elements. The sutures dividing these bones will be discussed later.

The prootic is a complex bone with five major processes. The terminology used by Mendrez (1972) to describe these processes will be followed here. The prootic meets the basisphenoid ventrally, the squamosal and opisthotic posterolaterally, the epipterygoid anterolaterally, and the supraoccipital dorsally.

In lateral view (Fig. 16), two distinct ridges can be seen running diagonally across the prootic, more or less parallel to each other. The ridge running from the central process to the anterodorsal process is here called the central ridge of the prootic (the 'delicate rising crest' of Mendrez 1972: 205). The ridge running from the lip of the fenestra ovalis to the anteroventral process of the prootic, is here called the ventral ridge of the prootic (the 'sharp crest'—Mendrez 1972: 203; the 'strong crest'—Mendrez 1972: 205; 1974b: 76).

In lateral view it can be seen that the prootic has two distinct anterior processes directed diagonally anterodorsally, viz: the anterodorsal process above and anteroventral process below. These two processes are separated by the incisura prootica. Olson (1944), Crompton (1955), Mendrez (1972) and others used these terms to describe the anterior part of the prootic.

The anterior part of the anterodorsal process makes contact with the medial surface of the epipterygoid, whereas the anteroventral process passes medially to the epipterygoid, forming a large vacuity between it and the epipterygoid—



Fig. 10. *Moschorhinus kitchingi*. BP/1/4636. Detail of left temporal region.



Fig. 11. *Moschorhinus kitchingi*. BP/1/4636. Dorsolateral view of left temporal region.

the cavum epiptericum, which will be discussed later. The anterodorsal process runs more or less parallel to the sagittal plane, whereas the anteroventral process points inwards.

The anterodorsal process of the prootic (processus anterior superior—Siebenrock 1893; posterior prootic process—Boonstra 1934) is a flattened, broad, projection that originates more or less in the middle of the prootic. Its dorsal border is continuous with the dorsal border of the rest of the prootic, and its ventral border is a continuation of the central ridge of the prootic. The anterodorsal process is rather broad posteriorly but tapers anteriorly, the thinnest part being its anterior edge, which contacts the posteromedial edge of the epipterygoid laterally. This region is damaged in the specimen described by Mendrez (1974a). The anteroventral edge of the anterodorsal process forms the posterior border of the posterior foramen of the epipterygoid. There is a slight lateral protrusion on the posterior part of the ventral border of the anterodorsal process, causing a ventrolaterally directed protuberance in the central ridge of the prootic. This is probably where the prootic made contact with the posterior apophysis of the epipterygoid, because of its inclination towards, and proximity to, the apophysis.

Bordering the anterodorsal process of the prootic dorsally and meeting the anterodorsal process of the epipterygoid is the flat, finger-like anterolateral process of the supraoccipital. The suture between the supraoccipital and prootic is not continuous. Posterior to the ventral edge of the posterodorsal process of the epipterygoid, a small triangular gap is formed between the supraoccipital and prootic. This is the dorsal venous foramen commonly found in many therapsids (see discussion).

The plane of the anterodorsal process is diagonally inclined in cross-section. The ventral border flares out laterally, whereas the dorsal border is medially inclined, reflecting the orientation of the epipterygoid.

The anteroventral process of the prootic (processus anterior inferior—Siebenrock 1893; anterior prootic process—Boonstra 1934) originates below the contact between the posterior apophysis of the epipterygoid and the anterodorsal process. This process is the ossified pila antotica (pleurosphenoid) (De Beer 1937; Olson 1944; Säve-Söderbergh 1947; Crompton 1955). The dorsal border of the anteroventral process curves upwards in a crescent shape. The anteroventral process is vertically inclined in cross-section and curves inwards anteriorly. The anteroventral process is traversed anteriorly by a horizontal groove. Above this shallow indentation, a low ridge runs from the posterior border of the incisura prootica anteriorly. This low ridge flares out anteriorly, forming two small, anteriorly jutting projections.

The incisura prootica is wide and deep. It is bordered ventrally by the concave dorsal border of the anteroventral process and dorsally by the straight ventral border of the anterodorsal process.

The foramen for the facial nerve (VII) is situated between the central and ventral ridges of the prootic. This foramen is nearer the former ridge and on the



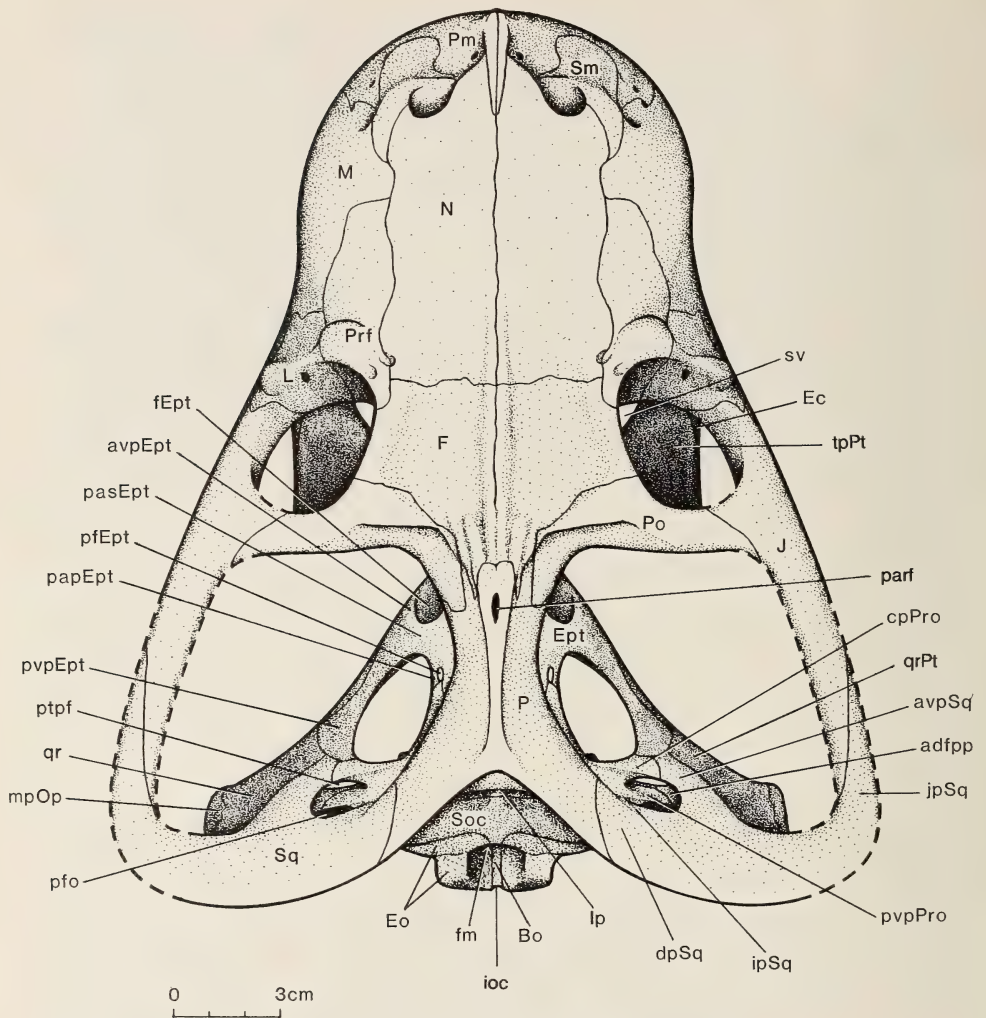


Fig. 12. *Moschorhinus kitchingi*. Dorsal view.

same level as the ventral border of the anteroventral process of the prootic anterior to it, and the central process of the prootic posterior to it.

There is a small ventral notch between the ventral border of the anteroventral process and the braincase floor. Its posterior border is formed by the anterior border of the basal region of the prootic. The ventral border is formed by the basisphenoid. This is the same as the notch described by Crompton (1955) for the Scalaposauridae, though here it is more open anteriorly.

The prootic has three prominent lateral processes of approximately the same length. The central process of the prootic (lateral process of the prootic—

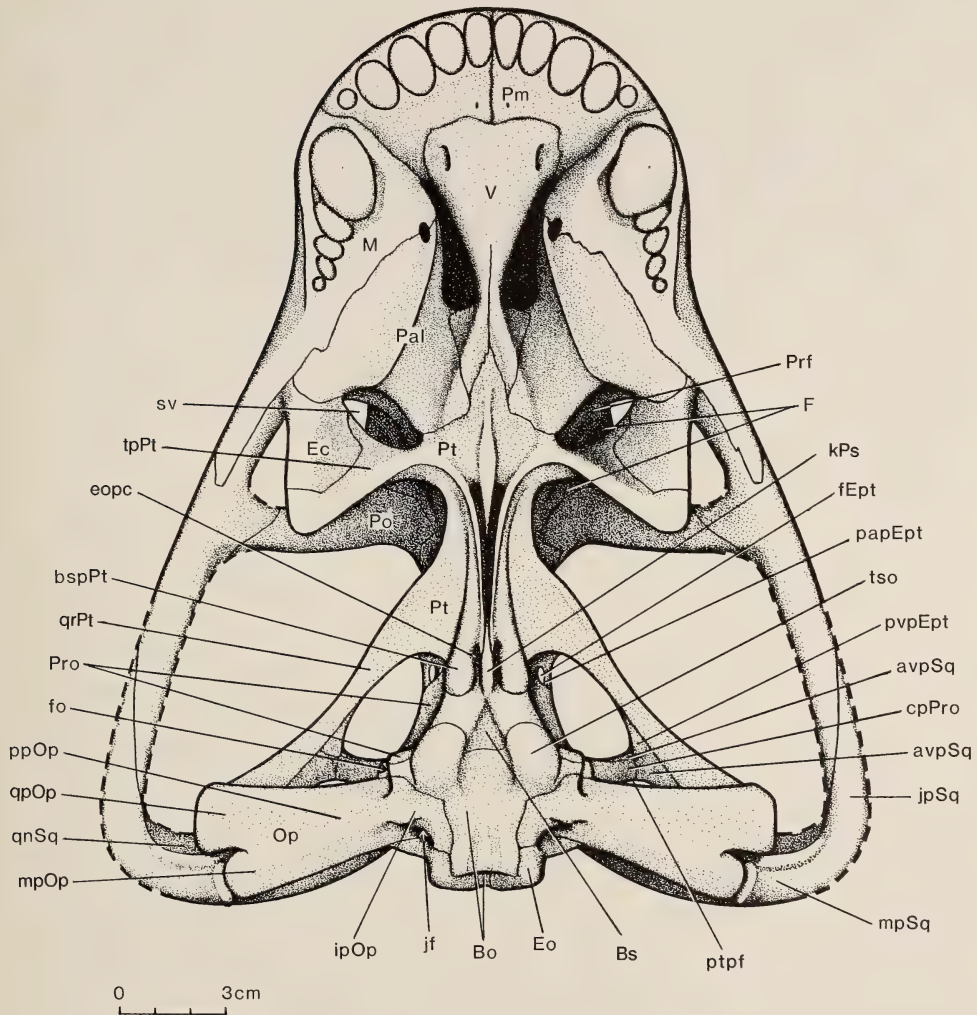


Fig. 13. *Moschorhinus kitchingi*. Ventral view.

Kemp 1972) can be seen in lateral (Fig. 16), dorsal, ventral and occipital views. It juts out laterally and slightly posteroventrally towards the squamosal. Its anterolateral corner contacts the posteromedial corner of the posteroventral process of the epitygoid. The medial part of the anteroventral process of the squamosal (prootic process of the squamosal—Mendrez 1974b) contacts this central process in a complex manner: the distal part of the central process forms two flanges, one anterodorsally, the other posteroventrally, between which the thin medial blade of the anteroventral process of the squamosal is wedged.

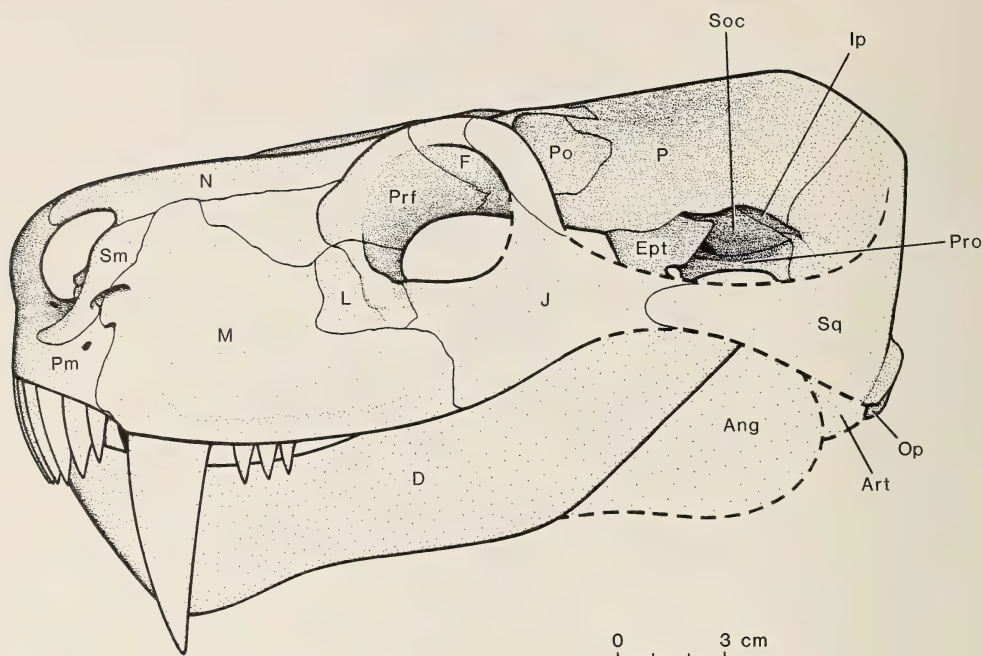


Fig. 14. *Moschorhinus kitchingi*. Lateral view.

These two elements form an anterodorsally curving bar that forms the anterior border of the pterygo-paroccipital foramen. The dorsal crest-like border of this bar is a continuation of the central ridge of the prootic. The anteroventral border of this bar forms a sharp concave crest running from the dorsal lip of the fenestra ovalis medially to the posteromedial corner of the posteroventral process of the epipterygoid laterally. The distal part of the central process is spindle-shaped in cross-section. The base of the central process, however, is triangular in cross-section, because of a short, sharp crest that forms the posteromedial corner of the process. This crest originates on the posteromedial part of the central process, curves posteromedially and terminates on the anterior surface of the posteroventral process of the prootic.

Behind the central process of the prootic, a more posteriorly inclined, flattened process, the posteroventral process of the prootic, originates. This process can be seen in occipital view. It contacts the opisthotic ventrolaterally. This unified structure forms the posterior wall of the pterygo-paroccipital foramen, the ventral border of the post-temporal fenestra and the anterior wall of the paroccipital fossa. The posteroventral process forms only the dorsomedial quarter of the posterior wall of the pterygo-paroccipital foramen and the medial half of the ventral border of the post-temporal fenestra.

A third process, the posterodorsal process of the prootic, contacts the intermediate process of the squamosal dorsally. It can be seen in lateral view



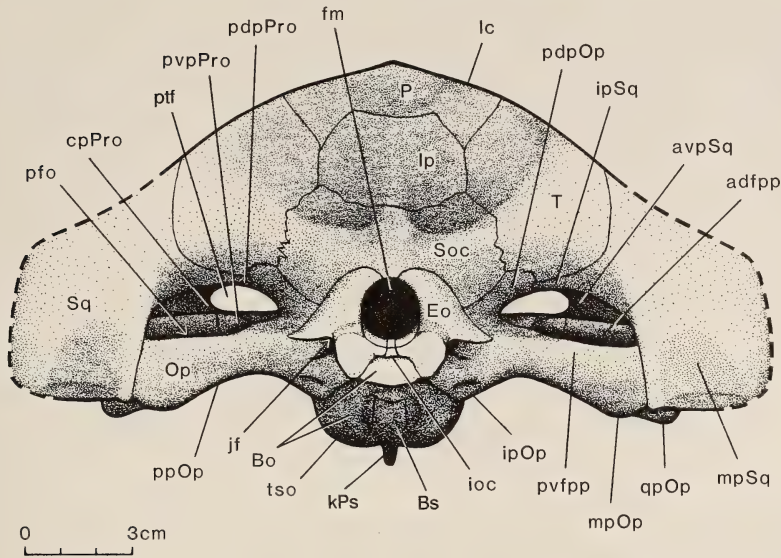


Fig. 15. *Moschorhinus kitchingi*. Occipital view.

(Fig. 16). The posterodorsal process forms most of the anterodorsal rim of the post-temporal fenestra. This process tapers off from a relatively broad base medially to a point jutting laterally, terminating in the lateral part of the roof of the post-temporal fenestra. This process protrudes from under the intermediate process of the squamosal anteromedially but, as it progresses laterally, it is gradually covered by the intermediate process of the squamosal anteriorly. Its posteromedial half is covered by the posterodorsal process of the opisthotic.

In lateral (Figs 16, 17) and ventral (Fig. 13) views, it can be seen that the basal region of the prootic is in sutural contact with the basisphenoid. The lateral suture runs diagonally from the floor of the braincase anterodorsally to the fenestra ovalis posteroventrally. The anterodorsal part of the lip surrounding the fenestra ovalis is formed by the basal region of the prootic (see Fig. 17).

As Mendrez (1972, 1974a) has remarked, the opisthotic and prootic are two quite separate bones. A clearly distinguishable suture divides them. The posterodorsal process of the opisthotic does not make contact with the lateral border of the posterodorsal process of the prootic, nor is it visible in anterior view as Mendrez (1974a) stated to be the case. The posterodorsal process of the opisthotic covers the posteromedial half of the posterodorsal process of the prootic posteriorly. In occipital view, one can observe within the post-temporal fenestra a part of the suture dividing the posterodorsal processes of the prootic and the opisthotic. This suture runs vertically for a short distance, skirting the lateral border of the posterodorsal process of the opisthotic, and then curves medially along its ventral border to where the posteromedial borders of the posteroventral and posterodorsal processes of the prootic originate. Laterally to

this, the suture divides the medial lip formed by the posteroventral process of the prootic and the posteroventral flange of the paroccipital process of the opisthotic. Ventrally to this medial lip, the suture that divides the posteroventral process of the prootic from the anterodorsal flange of the opisthotic, runs laterally. It can be traced posteriorly in the paroccipital fossa (Mendrez 1972: 203) and anteriorly between the anterodorsal flange of the paroccipital process of the opisthotic and the posteroventral process of the prootic. The suture curves first ventrally then medially along the border of the posteroventral process of the prootic. The suture then skirts the base of the central process of the prootic anteroventrally and the posterior corner of the dorsal lip of the fenestra ovalis, before it enters the roof of the fenestra ovalis medially (see Fig. 17).

The concave, dorsal border of the prootic can be seen in lateral view, curving posterodorsally to meet the medial border of the intermediate process of the squamosal. The central part of the dorsal border of the prootic (dorsal limit of the 'lame dorsale' of the prootic—Mendrez 1974a) contacts the supraoccipital. The largest part of the ventral border of the lateral supraoccipital fossa is formed by the dorsal border of the prootic. (This fossa is discussed below.)

#### OPISTHOTIC (Figs 12–17)

The opisthotic contacts the exoccipital and basioccipital posteromedially, the prootic anteromedially, the tabular, supraoccipital and squamosal dorsally, the squamosal, pterygoid and quadrate laterally, and the stapes ventrally.

The opisthotic consists of a robust transverse bar—the paroccipital process, a T-shaped ventromedial tuberosity—the internal process, and a small, flattened dorsomedial projection—the posterodorsal process. This is the terminology Mendrez (1972, 1974a, 1974b) used to describe the opisthotic.

The paroccipital process of the opisthotic is V-shaped in parasagittal section. This V-shaped process is formed by two flanges joined anteroventrally. The posteroventral flange is more massive than the anterodorsal flange. The V-shaped cavity formed by these two flanges is the paroccipital fossa of the opisthotic. This fossa can be seen in dorsal and occipital views (Mendrez 1972, 1974a, 1974b).

The paroccipital process is laterally subdivided into two processes that can be distinguished in ventral view, viz: the mastoid process of the opisthotic posteriorly, and the quadrate process of the opisthotic anteriorly (see Fig. 13).

The mastoid process is marked by a ventral ridge originating approximately in the middle of the paroccipital process and terminating near the bulbous lateral end of the mastoid process. This ventrolaterally curving ventral ridge adds to the robustness of the mastoid process. The mastoid process is thickest near its distal end where the ventral ridge terminates. The posterior margin of the mastoid process marks the posteroventral border of the rim of the paroccipital fossa. The posterolateral part of the mastoid process contacts the squamosal laterally, whereas its anterolateral part is free. A shallow indentation

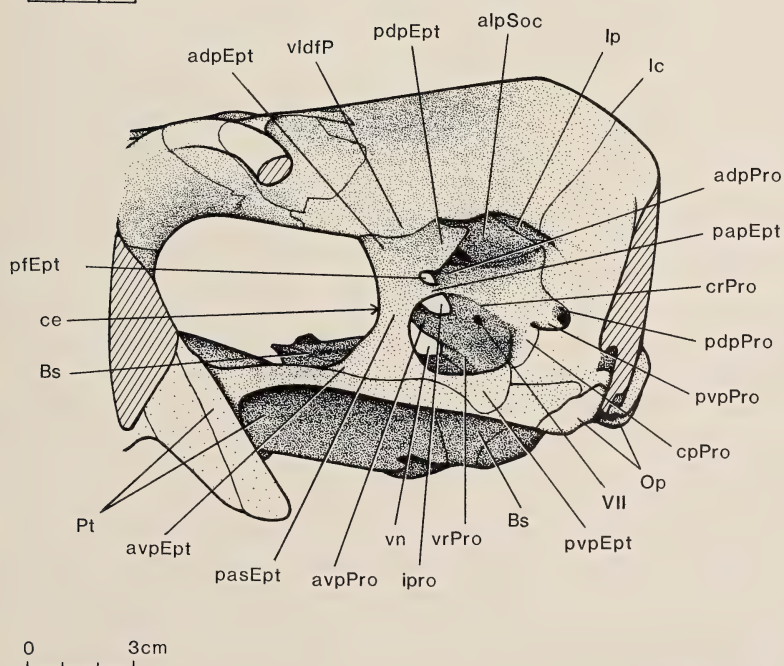
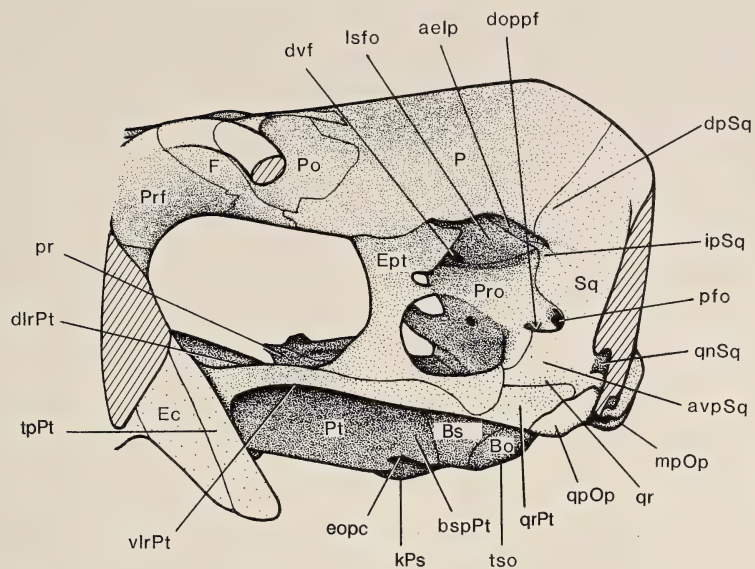


Fig. 16. *Moschorhinus kitchingi*. A. Detail of left temporal region. B. Detail of left temporal region.



separates the mastoid and quadrate processes of the opisthotic and forms the so-called roof of the middle ear ('toit de l'oreille moyenne'—Mendrez 1974a). The quadrate process of the opisthotic, which juts outwards anterolaterally, is thinner, broader and longer than the mastoid process. It becomes broader laterally, similarly to the mastoid process, to form a bulbous lateral end. The quadrate process projects further laterally than the mastoid process. The posterior third of the dorsolateral surface of the quadrate process of the opisthotic contacts the quadrate process of the squamosal and the anterior two-thirds contact the posterior part of the quadrate ramus of the pterygoid. This can be seen in lateral (Fig. 16) and dorsal (Fig. 12) views. The lateral surface of the quadrate process of the opisthotic loosely articulates with the quadrate and its anteroventral surface loosely contacts the stapes.

The anterodorsal flange of the paroccipital process (anterior wall of the paroccipital process—Mendrez 1972) contacts the posteroventral process of the prootic medially. This combined structure forms the posterior wall of the pterygo-paroccipital foramen (seen in dorsal view), the ventral border of the post-temporal fenestra and the anterodorsal border of the paroccipital fossa (both seen in occipital view). The anterior ridge of the paroccipital process, marking the anterior border of the opisthotic, originates at the anterolateral edge of the quadrate process of the opisthotic and terminates near the dorsal lip of the fenestra ovalis. The base of the central process of the prootic and the dorsal lip of the fenestra ovalis (also formed by the prootic) contact the anteromedial part of the opisthotic (see Fig. 17). The suture dividing the prootic and opisthotic has already been described.

The opisthotic forms the posterior third of the fenestra ovalis. The suture dividing the opisthotic and the basioccipital can be seen in ventral and occipital view. It emerges from the posteroventral corner of the fenestra ovalis and then turns medially across the ventral surface of the lip of the fenestra ovalis (Fig. 17). The suture then curves posteromedially behind the tuberculum spheeno-occipitale, runs around the internal process of the opisthotic and then curves laterally after passing medially to the jugular foramen. On reaching the posteroventral lip of the jugular foramen, the suture extends into the jugular foramen in an anterodorsal direction.

The internal process of the opisthotic can be seen in ventral and occipital views. It is formed by a ridge originating on the ventromedial part of the paroccipital process, curving and expanding ventromedially and terminating as a ventromedial tuberosity between the jugular foramen and fenestra ovalis. From this tuberosity a thin anterolateral and thicker, blunter posteromedial extension project. The posterior extension forms the ventral lip of the jugular foramen and the anterior extension forms the posteroventral corner of the lip of the fenestra ovalis (Fig. 17). There is a small groove dividing the anterior extension from the medial part of the opisthotic that forms the posterior border of the fenestra ovalis. Similarly the posterior extension is separated ventrally from the part of the opisthotic that forms the anterior part of the roof of the jugular foramen by

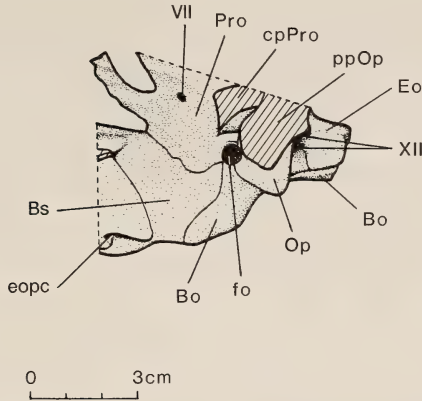


Fig. 17. *Moschorhinus kitchingi*. Detail of left fenestra ovalis.

a shallow groove (see Fig. 17). This groove runs from inside the jugular foramen anteromedially, more or less parallel to the ventrolateral suture of the exoccipital, and terminates on the posteromedial surface of the paroccipital process. The part of the opisthotic that is overlain by the posterior extension of the internal process projects into the jugular foramen and, with the exoccipital posteriorly, forms the roof of the jugular foramen. A short groove is present on the posterior face of the ridge and tuberosity, ventral to the groove at the jugular foramen (see Figs 13, 15).

In occipital view, the suture between the anterolateral part of the exoccipital and the posteromedial surface of the opisthotic can be seen. This suture runs from inside the jugular foramen, around the exoccipital ventrolaterally, and then dorsomedially. Also visible in occipital view is the suture dividing the medial corner of the posterodorsal process of the opisthotic and the ventrolateral corner of the supraoccipital. It originates half-way along the dorsal border of the exoccipital.

The posterodorsal process of the opisthotic (visible in occipital view) originates medially to the paroccipital fossa and the lip (formed by the posteroventral process of the prootic and the posteroventral flange of the paroccipital process) covering the dorsomedial part of the paroccipital fossa. The posterodorsal process of the opisthotic is a flat projection that curves dorso-laterally. It forms the posteromedial surface of the post-temporal fenestra. Its lateral border stretches as far medially as the lip covering the dorsomedial part of the paroccipital fossa (a medial indentation separates these two structures). The posterodorsal process of the opisthotic makes sutural contact along its dorsomedial border with the supraoccipital. This suture continues in a dorso-lateral direction as it follows the dorsal border of the posterodorsal process. The suture dividing the supraoccipital and tabular originates half-way along this border. Part of the dorsal border of the posterodorsal process contacts the

ventral border of the tabular. The lateral border of the posterodorsal process contacts the posteroventral part of the intermediate process of the squamosal. The short ventral border of the posterodorsal process of the opisthotic contacts the posterior part of the posterodorsal process of the prootic. The posterodorsal process of the opisthotic is not visible in anterior view as Mendrez (1974a) has observed in *Moschorhinus kitchingi*, SAM-K118. It rather resembles the condition found by Mendrez (1974b) in *Promoschorhynchus platyrhinus*, RC 116, where the posterodorsal process is completely covered anteriorly by the intermediate process of the squamosal and the anterodorsal process of the prootic.

#### SQUAMOSAL (Figs 12–16)

The squamosal is a large, complex bone with several processes; the terminology used by Mendrez (1972) will be used to describe these processes. The squamosal makes contact with the parietal, interparietal, supraoccipital, prootic, opisthotic and tabular medially, the pterygoid and epipterygoid anteriorly, and with the jugal and quadrate laterally.

The major part of the posterior wall of the temporal fossa is formed by the three large medial processes of the squamosal. The laterally sloping dorsal border of the squamosal forms the posterodorsal border of the temporal fossa and anterior part of the lambdoid crest. The three medial processes occur one above the other (see Fig. 16). The anteroventral process (third squamosal process—Crompton 1955) is separated from the intermediate process (second squamosal process of Crompton) by the post-temporal fenestra. The intermediate and dorsal processes (first squamosal process of Crompton) are separated by the posterior fold forming part of the lateral supraoccipital fossa.

The medial part of the broad dorsal process of the squamosal covers the posterolateral part of the parietal (see Fig. 12). The lateral surface of the dorsal process is confluent with that of the parietal, as are their dorsal and ventral borders. The dorsal process of the squamosal is fused to the tabular along most of its posterior surface. Its ventral border is marked by the fold forming the posterior part of the lateral supraoccipital fossa (see Fig. 16). Part of this fold is occupied by the anterior extension of the interparietal, which contacts the ventral border of the dorsal process posterodorsally.

In lateral view it can be seen that the dorsal border of the intermediate process of the squamosal forms the ventral border of the above-mentioned fold and contacts the posteroventral area of the part of the interparietal that is laterally exposed. The anterior part of the intermediate process makes sutural contact with the anterolateral process of the supraoccipital dorsally and with the prootic ventrally. The medial part of the ventral border of the intermediate process of the squamosal forms a V-shaped notch in which the posterodorsal process of the prootic is wedged. This fused structure forms the dorsomedial part of the roof of the post-temporal fenestra, whereas the dorsolateral part of the roof is formed by the lateral part of the ventral border of the intermediate process.



In occipital view it can be seen that the medial part of the intermediate process contacts the ventrolateral part of the tabular, and the dorsolateral part of the posterodorsal process of the opisthotic ventromedially.

In lateral view the ventral border of the intermediate process can be seen. It curves ventrolaterally in a crescent-shape, delimiting the dorsolateral rim of the post-temporal fenestra, until it becomes the dorsal border of the anteroventral process of the squamosal. The dorsal border of the anteroventral process forms the lateral part of the pterygo-paroccipital foramen. The medial blade of the anteroventral process of the squamosal (the prootic process of the squamosal—Mendrez 1974*b*) is wedged into a V-shaped notch formed by the lateral part of the central process of the prootic. The posteromedial border of the posteroventral process of the epipterygoid contacts the anteroventral process of the squamosal anteromedially. The whole anterolateral border of the anteroventral process of the squamosal, except for its distal end, contacts the posteromedial edge of the quadrate ramus of the pterygoid. This suture runs posterolaterally from the contact between the posterior part of the posteroventral process of the epipterygoid and the squamosal, to the suture connecting the squamosal and opisthotic.

The laterally directed flange of the squamosal overlies most of the opisthotic, the only contact formed being where their distal borders meet (see Fig. 15). The ventrolateral part of the anteroventral process of the squamosal (the quadrate process of the squamosal—Mendrez 1974*b*) contacts the dorsal part of the posterolateral tip of the quadrate process of the opisthotic posterior to the squamosal-ptyerygoid contact (see Fig. 16). This suture is visible anteriorly to the quadrate notch in the squamosal. (This notch is described below.) The ventrolateral part of the squamosal seen in occipital view is the mastoid process of the squamosal. The suture connecting the dorsolateral border of the mastoid process of the opisthotic to the ventromedial border of the mastoid process of the squamosal is visible in occipital and ventral views. Except for these two above-mentioned distal sutures and the suture with the posterodorsal process of the opisthotic, the rest of the squamosal overlies, but does not contact, the opisthotic. It thus forms the lateral parts of the roof of the pterygo-paroccipital foramen and the roof of the paroccipital fossa.

A deep, dorsally directed quadrate notch of the squamosal is present anteriorly, in the distal part of the squamosal; it houses the dorsal part of the quadrate (see Fig. 16). This notch is surrounded by the jugal laterally, the posterolateral part of the anteroventral process of the squamosal (which covers the quadrate process of the opisthotic) anteroventrally and the thick lip formed by the jugal process of the squamosal dorsally. A shallow indentation is present anteroventrally to this notch in the bones covering the quadrate process of the opisthotic, namely, the quadrate process of the squamosal and the posterior end of the quadrate ramus of the pterygoid. This indentation, the quadrate recess of the squamosal, is probably synonymous with that described by Kemp (1969) and with the squamosal recess ('recessus squamosal') of Mendrez (1974*a*). The

posterior part of the quadrate fits into this recess. The quadrates are lost in most of the *Moschorhinus* specimens, because they were loosely articulating bones with no sutural connections.

In occipital view the following features can also be seen: the posteroventral border of the intermediate process of the squamosal curves ventrolaterally, forming the posterolateral border of the post-temporal fenestra and part of the posterolateral border of the paroccipital fossa. A ridge runs in a dorso-ventral plane on the mastoid process of the squamosal laterally to its contact with the opisthotic. A posteroventral facing indentation on the mastoid process of the squamosal borders this ridge laterally. Ventrally to this indentation and ridge, and medially to the posterior part of the quadrate, a notch is situated posteriorly between the two lateral processes of the opisthotic.

The dorsolateral part of the squamosal (the jugal process) curves anteriorly to join the posterior end of the jugal. Unfortunately, in those specimens studied, the jugal arch is either lost or damaged to such a degree that a detailed description is impossible.

#### SUPRAOCCIPITAL AND INTERPARIETAL (Figs 14, 15)

Both the supraoccipital and the interparietal are visible in occipital and lateral view. In occipital view, the broad supraoccipital contacts the interparietal dorsally, the tabulars dorsolaterally, the posterodorsal processes of the opisthotics ventrolaterally and the exoccipitals ventrally. The exoccipitals cover the ventromedial part of the supraoccipital, except for a narrow gap between the exoccipitals where the supraoccipital forms the dorsomedial part of the roof of the foramen magnum. The suture between the tabular and supraoccipital runs diagonally in a dorsomedial direction from its origin at the junction of the ventral borders of the tabular and supraoccipital, to the dorsal border of the supraoccipital. The suture between the ventral border of the interparietal and the dorsal border of the supraoccipital is horizontal and short. A large, deep occipital indentation is present in the region of the interparietal. Two smaller, ventral indentations, forming part of the larger indentation, are present on the dorsal part of the supraoccipital. These flank a short ridge originating in the middle of the dorsal part of the supraoccipital and continuing dorsally on the interparietal.

In occipital view, the interparietal is a small, laterally ovate bone bordered ventrally by the supraoccipital, laterally by the tabulars and dorsally by the parietal.

The aforementioned occipital indentation causes the interparietal, parietal, medial part of the tabular, and the dorsal part of the supraoccipital to be set deeper than the rest of the surrounding elements. This indentation was for the attachment of certain neck muscles.

In lateral view, ventral to the posteromedial angle of the temporal foramen (Mendrez 1974a: 80), is the lateral supraoccipital fossa, a large oval indentation bordered dorsally by the parietal, whose ventral border forms a concave over-

hang. The ventral border of this fossa is formed by the concave dorsal edge of the anterodorsal process of the prootic, and the anterior border by the anteroventrally curving posterior edge of the posterodorsal process of the epipterygoid. The fossa tapers off posteriorly into a short, horizontal fold. The anteromedial part of the intermediate process of the squamosal forms the posterior border of the fossa and the ventral part of its posterior fold. The dorsal border of this fold is formed by the ventral border of the parietal and the dorsal process of the squamosal. The dorsal venous foramen is situated in the anterior region of this fossa.

The anterior extensions of the supraoccipital and interparietal are visible within the lateral supraoccipital fossa. The anterolateral process of the supraoccipital lies at a more medial level than any of the surrounding elements, forming the medial wall of the lateral supraoccipital fossa. The anterolateral process of the supraoccipital contacts the parietal dorsally, the posterodorsal process of the epipterygoid anteriorly, the anterodorsal process of the prootic ventrally, the intermediate process of the squamosal posteroventrally, and the anterior extension of the interparietal posterodorsally. The dorsal venous foramen is visible ventral to the epipterygoid-supraoccipital contact and anterior to the prootic-supraoccipital contact.

The anterior extension of the interparietal fills the posterodorsal corner of the lateral supraoccipital fossa. The interparietal is triangularly shaped and contacts the anterolateral process of the supraoccipital anteroventrally, the dorsal border of the intermediate process of the squamosal posteroventrally, the ventral border of the parietal anterodorsally, and the ventral border of the dorsal process of the squamosal posterodorsally.

#### PARIETAL (Figs 12, 14–16)

The parietal forms the posterodorsal part of the skull. It contacts the squamosal and tabular posteroventrally, the prootic and epipterygoid ventrolaterally, the postorbital anterolaterally, and the frontal anteriorly.

In occipital view the parietal is situated between the dorsomedial borders of the tabulars and the dorsal border of the interparietal. Its dorsal border is in confluence with those of the tabular and squamosal. These borders form the ventrolaterally curving, dorsal border of the occiput.

The parietal has a pronounced sagittal crest. The anterodorsal rim of the temporal fossa is formed by an acute curving ridge on the posterodorsal and dorsolateral surfaces of the postorbital (see Fig. 12). These postorbital ridges bow posteriorly and are continued on the dorsomedial surface to produce the sagittal crest. The sagittal crest is widest at its origin, anterior to the parietal foramen. Posteriorly it becomes narrower and splits into two posterolaterally flaring lambdoid crests, which form the dorsomedial border of the occiput posteriorly and part of the posterodorsal rim of the temporal fossa laterally.

The parietal, in dorsal view, has an hour-glass shape. It is broad and robust anteriorly, constricted in the middle above the epipterygoid, and forms two



posterolaterally flaring flanges that form the anterior parts of the lambdoid crests.

The broad anterior part of the parietal contacts the frontal and postorbitals (see Figs 12, 14, 16). In dorsal view, it can be seen that the suture between the posterodorsal border of the frontal and the anterodorsal border of the parietal has a zig-zag arrangement. The anteroventrally sloping area between the anterior border of the parietal and the parietal foramen, i.e. the broad origin of the sagittal crest, is corrugated. In BP/1/4636, four small but distinct parasagittal ridges are present in this region. The two medial ridges join up with the sagittal ridge of the frontal anterior to them. This sagittal ridge runs on the dorsal surface of the skull, from the middle of the nasals, over the frontals, and joins the medial ridges of the parietal, which terminate on the slope anterior to the parietal foramen.

The posteromedial flange of the postorbital and the anterolateral part of the parietal are separated by a suture that can be seen in dorsal and lateral view.

The parietal foramen for the pineal organ is situated in the anterior part of the sagittal crest, on the same level as the posterior border of the posteromedial flange of the postorbital (see Fig. 12). The external opening of the parietal foramen is a narrow spindle-shaped slit, similar to the condition in the *Moschorhinus* specimens described by Brink (1959) and Mendrez (1974a).

In lateral view, the vertically curving suture between the dorsal process of the squamosal and the posterior flange of the parietal can be seen. This suture closely reflects the occipital suture between the parietal and interparietal and the tabular. The ventral border of the parietal forms the roof of the braincase. The anterior third of the ventral border of the parietal does not make sutural contact with any bony elements, since this part of the braincase was unossified. The middle part of the parietal is triangular in cross-section. The lateral edges of the ventral border of this triangle contact the dorsal border of the epipterygoid and the dorsal part of the anterolateral process of the supraoccipital on each side. The short ventrolateral descending flange of the parietal overlaps the anterior two-thirds of the dorsal border of the epipterygoid. The posterior part of the ventral area of the parietal contacts the dorsal border of the interparietal. The ventrolateral edge of the parietal, posterior to its suture with the epipterygoid, forms the dorsal border of the lateral supraoccipital fossa.

#### EXOCCIPITAL (Figs 12, 13, 15, 17)

In occipital view, it can be seen that the exoccipital contacts the posteroventral part of the supraoccipital dorsally, the posteromedial part of the opisthotic laterally, and the posterior part of the basioccipital ventromedially. The concave medial side of the exoccipital forms the lateral wall of the foramen magnum.

The exoccipital is divided externally into a flat anterodorsal part and a posteroventral boss. The ventrolateral half of the anterodorsal part overlaps the posteromedial part of the opisthotic and the dorsolateral half contacts the

posteroventral part of the supraoccipital. The anterodorsal part has two pronounced, acute rims; one medially, the other ventrally. The medial rim forms the dorsolateral lip of the foramen magnum. The ventral rim forms a ridge demarcating the posterodorsal lip of the jugular foramen.

The posteroventral bosses of the exoccipitals form, together with the posterior part of the basioccipital, the occipital condyle. The exoccipitals form the dorsolateral parts of the occipital condyle and the basioccipital the ventral third. The occipital condyle in BP/1/4636 has a central indentation on its articular surface, not described before in *Moschorhinus* (Figs 12, 15). This indentation involves the posterodorsal part of the basioccipital third of the condyle and the posteromedial parts of the exoccipitals. The indentation and the associated lateral bosses hint at a double condyle condition, and are similar to those described by Watson (1913). The suture dividing the exoccipital and the basioccipital runs parasagittally from dorsomedially inside the foramen magnum (see Fig. 12), over the dorsal rim of the occipital condyle, and diagonally to a point ventrolaterally on the convex ventral rim of the occipital condyle. From here the suture runs anteriorly for a short distance on the ventral surface of the occipital condyle and then curves dorsolaterally, over the ventromedial lip of the jugular foramen, from whence it plunges into the jugular foramen in an anterodorsal direction. The dorsomedial side of the posteroventral boss of the exoccipital forms the posterior part of the ventrolateral wall of the foramen magnum (and the concave dorsomedial border of the occipital condyle), and its posterodorsal rim demarcates the posterior border of the foramen magnum. The ventrolateral side of the posteroventral boss forms the ventrolateral border of the occipital condyle, and the anterior border of the ventrolateral side forms the posterior lip of the jugular foramen (Fig. 13). Near the mouth of the jugular foramen, the lateral wall of the posteroventral boss is penetrated by two small foramina for the hypoglossal nerve (XII) (see Fig. 17).

#### BASIOCCIPITAL (Figs 12, 13, 15–17)

The basioccipital forms the posterior part of the basicranium and the ventral part of the occiput. In ventral view, the basioccipital contacts the basisphenoid anteriorly, the opisthotic laterally, and the exoccipitals posterolaterally.

The anteroventral part of the basioccipital and the posteroventral part of the basisphenoid form the two spheno-occipital tubercles. The suture between the anterior border of the basioccipital and posterior border of the basisphenoid can be seen in ventral view. It dips diagonally in an anteroventral direction from the ventral lip of the fenestra ovalis, curves medially, and surrounds the posterior part of the spheno-occipital tubercle. The suture in the indentation between the two tubercles is set further posteriorly than those parts that bisect the tubercles.

Of the four elements that form the lip surrounding the fenestra ovalis, viz: the basioccipital, opisthotic, basisphenoid and prootic, the basioccipital

contributes least to the formation thereof after the basisphenoid (see Fig. 17). Posterolateral to each speno-occipital tubercle occurs the small laterally directed process of the basioccipitals that forms part of the ventral lip of the fenestra ovalis. This small process is wedged between the posterolateral corner of the basisphenoid anteriorly and the anterior border of the internal process of the opisthotic posteriorly.

The suture between the internal process of the opisthotic and the basioccipital has a roughly diagonal arrangement. Seen in ventral view, it emerges from the fenestra ovalis and runs medially across its ventral surface for a short distance. The suture turns posteromedially and skirts the anterolateral extension of the internal process of the opisthotic, then curves slightly posterolaterally around the ventromedial tuberosity and the posteromedial extension of the internal process of the opisthotic.

Between the posterior border of the internal process of the opisthotic and the posteroventral edge of the occipital condyle, a short parasagittal flange separates the ventrolateral border of the basioccipital and the ventromedial border of the occipital boss of the exoccipital. This suture can be seen in ventral view.

The posterior part of the basioccipital has a rugose ventral surface. This rectangular part of the basioccipital, situated posteriorly to the level of the jugal foramina, forms the convex base of the occipital condyle.

In dorsal view, the posterior part of the basioccipital that participates in the formation of the occipital condyle is visible as a thin strip flanked by the posteroventral bosses of the exoccipitals. The basioccipital is wedge-shaped in occipital view; the broad concave base of the wedge is formed by the ventral surface of the basioccipital. The suture between the basioccipital and exoccipital has been described above.

## DISCUSSION

In his paper on the Scaloposauridae, Crompton (1955) described a fused periotic and mentioned that Olson (1944) had not found any dividing suture in the periotic of those therocephalians he had studied either. The specimen known as 'Therocephalian A' (Olson 1944) was discovered in the *Tapinocephalus* zone. Its locality (Boonstra 1969; Kitching 1977) and size indicate that it is most probably a pristerognathid. Olson (1938b) described this specimen as having a periotic, but Boonstra (1954) and Van den Heever (pers. comm.) found a prootic and opisthotic in the Pristerognathidae. It has been shown by Van den Heever & Hopson (1982) that 'Therocephalian B' (Olson 1944) is actually a gorgonopsian. Olson (1944) described a periotic in this specimen, as well as in the other gorgonopsians he studied. Authors such as Sigogneau (1970, 1974) described a prootic and opisthotic in the Gorgonopsia. However, it is possible that, in certain adult Gorgonopsia and Pristerognathidae, the suture between the prootic and opisthotic is difficult or impossible to detect in the region sur-



rounding the fenestra ovalis, but the co-ossification of these elements is not complete enough to consider these groups as having a periotic. The Scaloposauridae also have an opisthotic and prootic as described by Mendrez (1972), and not a periotic as Crompton (1955) described. Neither the Whaitsiidae (pers. obs.) nor the Moschorhinidae have a periotic, a clearly distinguishable prootic and opisthotic being present. It seems quite clear that the Therocephalia have a prootic and opisthotic, and not a periotic.

The pterygoid process of the quadrate, as it is described by Mendrez (1974a), is actually not part of the quadrate but is the posterior end of the quadrate ramus of the pterygoid. The quadrates have been lost in the *Moschorhinus kitchingi* specimen described by Mendrez (1974a) and the specimens described here.

Judging from the shape of the squamosal recess, the quadrate was a relatively large, broad bone, approximately the same shape and size as that described by Mendrez (1974b) in *Promoschorhynchus platyrhinus*. In contrast to the condition understood in *Promoschorhynchus*, the quadrate in *Moschorhinus* seems to have had a small dorsal process that fitted into the quadrate notch of the squamosal (described below). This notch and slot arrangement allowed the quadrate to articulate with the squamosal in a hinge-like manner. The quadrate lay upon the quadrate process of the squamosal and the lateral tip of the quadrate process of the opisthotic that is not covered by the squamosal or pterygoid.

The shape of the quadrate notch of the squamosal indicates that the quadrate had a posterolaterally directed process that articulated medially with the lateral end of the quadrate process of the opisthotic and the quadrate process of the squamosal, and posteriorly with the posterior wall of the quadrate notch that is formed by the squamosal. This process is probably synonymous with the 'squamosal process of the quadrate' described by Mendrez (1974b) in *Promoschorhynchus platyrhinus*. The posteroventral part of the quadrate probably contacted the squamosal in the same manner as in *Promoschorhynchus*. If this was the case, the stapes would be longer than Mendrez (1974a) indicated in *Moschorhinus kitchingi*, and would extend laterally past the lateral end of the opisthotic. The lateral side of the quadrate would have contacted the medial part of the quadratojugal. Because of the absence of the stapes and quadratojugal, it is not possible to describe the relations between these elements and the quadrate.

In her paper on *Moschorhinus*, Mendrez (1974a) referred to the opening dorsal to the posterior apophysis of the epipterygoid and the anterodorsal process of the prootic as the 'foramen veineux'. It would seem that the dorsal part of the anterodorsal process of the prootic is damaged in her specimen. The posterior foramen of the epipterygoid and dorsal venous foramen are separated by the anterodorsal process of the prootic. This process is expanded dorsally to contact the supraoccipital and the posterodorsal process of the epipterygoid. (The term 'dorsal venous foramen' is preferred to venous notch—Boonstra 1934; Cox 1959; dorsal notch—Mendrez 1972; and venous foramen—Mendrez

1974*b*, because it is a foramen completely surrounded by bone, and distinguishes between the two above-mentioned venous foramina.)

The root of the trigeminal nerve (V) exits through the incisura prootica into the cavum epiptericum, which housed the trigeminal ganglion. From this ganglion the three trigeminal rami branched. The ramus ophthalmicus passed mesial to the processus ascendens of the epipterygoid into the orbit. The ramus maxillaris and ramus mandibularis passed posterior to the processus ascendens into the temporal cavity (see Presley & Steel 1976). Certain authors (Brink 1957; Mendrez 1972, 1974*a*, 1974*b*) argue that the posterior apophysis of the epipterygoid divided these two rami. Others (Watson 1920; Kemp 1972) argued that both rami emerged through the foramen dorsal to the posterior apophysis (the posterior foramen of the epipterygoid). Crompton (1955) proposed a third alternative, namely that both rami emerged ventral to the posterior apophysis. The greatest part of the cavum epiptericum (and therefore also the trigeminal ganglion) lies below the level of the posterior foramen of the epipterygoid. Since the ramus maxillaris must have been directed ventrally, as is the ramus mandibularis, it is unlikely that it would first be deflected dorsally from the ganglion to pass through the posterior foramen of the epipterygoid and then ventrally towards the maxilla. It is more feasible that the ramus maxillaris passed, together with the ramus mandibularis, ventral to the posterior apophysis.

The root of the abducens nerve (VI) usually exits through a foramen in the base of the anteroventral process of the prootic (ossified pila antotica) (see Haughton 1918; Goodrich 1958; Starck 1979). In *Moschorhinus* (Mendrez 1974*a*; pers. obs.) and *Promoschorhynchus* (Mendrez 1974*b*) this foramen is absent. Olson (1938*a*) mentioned that a foramen for the abducens nerve may be absent in certain gorgonopsids and would, in this case, pass anterior to the prootic. This seems to have been the case in *Moschorhinus* as well.

The root of the facial nerve (VII) exits through its foramen between the central and ventral ridges of the prootic. No impression for the geniculate ganglion (gasserian ganglion—Mendrez 1972) could be found on the lateral surface of the prootic.

There is no separate glossopharyngeal foramen in *Moschorhinus*. The glossopharyngeal (IX) exited through the jugular canal together with the vago-accessory (X and XI). This is a common feature in the therapsids (see Watson 1911; Haughton 1918; Kemp 1979). The hypoglossal (XII) enters into the jugular foramen through two foramina in its dorsomedial wall (see Fig. 17).

The primary head vein of *Moschorhinus* probably ran mesially to the epipterygoid (see Goodrich 1958; Presley & Steel 1976), then laterally to the otic capsule where it received the vena cerebralis media. This united vessel passed ventral to the paroccipital process of the opisthotic (see Presley & Steel 1976). It is postulated that the vena cerebralis media most probably exited through the incisura prootica via the posterior foramen of the epipterygoid. The posterior foramen of the epipterygoid coincides with the dorsal part of the incisura

prootica, as the anteroventral border of the anterodorsal process of the prootic forms the foramen's posterior border (see Fig. 16). If the vena cerebialis media passed through this foramen, it would be in line with the dorsal opening of the pterygo-paroccipital foramen through which it would pass ventrally to join the primary head vein. Many authors (Watson 1920; Parrington 1946; Cox 1959; Fourie 1974) described a groove running from the pterygo-paroccipital foramen to the incisura prootica (foramen for the trigeminal nerve—Parrington 1946). Most authors since Watson (1920) have claimed that the vena capitis lateralis ran in this groove, but it seems unlikely that this large vein could pass through the small posterior foramen of the epipterygoid in *Moschorhinus*. Moreover, the vena cerebialis media, which is a very important vein in extant reptiles (usually ignored by these writers), must have left some trace on the lateral wall of the prootic.

The vena capitis dorsalis, which was situated in the sinus canal in cynodonts (Watson 1911), seems to have been expanded anteriorly to form a broad sinus that was situated in the lateral supraoccipital fossa in *Moschorhinus*. This sinus would have been confluent anteriorly with a vein that passed through the dorsal venous foramen. The vena capitis dorsalis would have been connected to the vein that passed through the pterygo-paroccipital foramen (probably the vena cerebialis media) and the vein that passed through the post-temporal fenestra (see Watson 1920; Parrington 1946; Cox 1959; Fourie 1974).

The internal carotid artery ran anteriorly, ventral to the paroccipital process of the opisthotic, and entered the external opening of the parabasal canal. The stapedia artery branched off from the internal carotid in the proximity of the stapes. It probably ran in an anterodorsal direction in the depression below the central ridge of the prootic towards the cavum epipterygium, where it ramified into three branches, each of which accompanied a trigeminal nerve ramus (see O'Donoghue 1920).

*Moschorhinus* has many primitive characteristics, such as large suborbital vacuities similar to those of the pristerognathids (see Boonstra 1969), a gorgonopsid-like dentition (see Parrington 1955), and a robust skull compared to other Therocephalia (see Crompton 1955; Romer 1956; Brink 1959). Its epipterygoid is not as expanded, and therefore not involved to the same degree in the formation of the lateral wall of the braincase as are those of *Promoschorhynchus* (Mendrez 1974b) or whaitsiids (Kemp 1972). No ossified ethmoid or orbitosphenoid elements could be found, as in gorgonopsids (see Olson 1944; Kemp 1969) or in whaitsiids (see Kemp 1972). *Moschorhinus* has large post-temporal fenestrae compared to cynodonts (see Watson 1920; Romer 1969; Kemp 1979), but this may be a characteristic peculiar to the Therocephalia (see Kemp 1972) because they are also larger than those of primitive therapsids (see Romer 1956).

Derived and advanced characteristics in *Moschorhinus* include the paroccipital fossa of the opisthotic, which seems to be shared with all the other therocephalians except the pristerognathids (see Hopson & Barghusen 1986).



The epipterygoid and its relations with the surrounding bony elements are more advanced in *Moschorhinus* than in primitive Therocephalia (see Boonstra 1934; Crompton 1955; Mendrez 1972). *Moschorhinus* has a much larger epipterygoid than the gorgonopsids, scaloposaurids or certain pristerognathids. Its epipterygoid makes sutural contact with the parietal and supraoccipital dorsally and the prootic posterodorsally, thus forming a substantial part of the lateral wall of the braincase. The posterior apophysis of the epipterygoid is present in certain Therocephalia (see Brink 1957; Kemp 1972; Mendrez 1974*b*), but in *Moschorhinus* it most probably made contact with the prootic, a condition unique amongst the Therocephalia. The posterior foramen of the epipterygoid is shared with the whaitsiids (see Kemp 1972). The venous notch of the primitive therapsids (see Boonstra 1934; Olson 1937; Mendrez 1972) is closed anteriorly by the epipterygoid in *Moschorhinus* forming a venous foramen, as happens in whaitsiids (see Kemp 1972).

Looking at all the above-mentioned characteristics it would seem that *Moschorhinus* was more advanced than the pristerognathids or scaloposaurids. *Moschorhinus* was more primitive than, but not ancestral to, the whaitsiids. *Moschorhinus* has a more primitive palatine region (see Mendrez 1974*a*), large suborbital vacuities, postcanines, and a robust skull. *Theriognathus*, on the other hand, does not possess suborbital vacuities nor postcanines and has a more delicate skull. *Moschorhinus* did not have an ossified orbitosphenoid or interorbital septum as in whaitsiids. Its epipterygoid is also much smaller and participates less in the formation of the lateral wall of the braincase (see Kemp 1972). The posterior foramen of the epipterygoid may have a different function in *Moschorhinus* than in whaitsiids, because in *Moschorhinus* it is formed differently and the posterior apophysis in the whaitsiid described by Kemp (1972) obstructs the passage between the posterior epipterygoid foramen and the pterygo-paroccipital foramen. In whaitsiids the posteroventral process of the epipterygoid (quadrate ramus of the pterygoid—Kemp 1972) is also apparently much closer to the prootic than in *Moschorhinus*.

*Moschorhinus* has too many derived characteristics to be a cynodont ancestor. It has paroccipital fossae, large post-temporal fenestrae and suborbital vacuities. It has few postcanine teeth, a small dorsal parietal foramen and, as in all Therocephalia, no stapedial foramen (see Mendrez 1974*a*). Furthermore, the posterior epipterygoid foramen is unique to the moschorhinids and the whaitsiids, and not homologous to the cynodont trigeminal foramen.

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## ABBREVIATIONS

adfpf	—anterodorsal flange of the paroccipital process	Op	—opisthotic
adpEpt	—anterodorsal process of the epipterygoid	P	—parietal
adpPro	—anterodorsal process of the prootic	Pal	—palatine
aeIp	—anterior extension of the interparietal	papEpt	—posterior apophysis of the epipterygoid
alpSoc	—anterolateral process of the supraoccipital	parf	—parietal foramen
Ang	—angular	pasEpt	—processus ascendens of the epipterygoid
Art	—articular	pdpEpt	—posterodorsal process of the epipterygoid
avpEpt	—anteroventral process of the epipterygoid	pdpOp	—posterodorsal process of the opisthotic
avpPro	—anteroventral process of the prootic	pdpPro	—posterodorsal process of the prootic
avpSq	—anteroventral process of the squamosal	pfEpt	—posterior foramen of the epipterygoid
Bo	—basioccipital	pfo	—paroccipital fossa
Bs	—basisphenoid	Pm	—premaxilla
bspPt	—basisphenoid process of the pterygoid	Po	—postorbital
ce	—cavum epiptericum	ppOp	—paroccipital process of the opisthotic
cpPro	—central process of the prootic	pr	—parasphenoid rostrum
crPro	—central ridge of the prootic	Prf	—prefrontal
D	—dentary	Pro	—prootic
dlrPt	—dorsolateral ridge of the pterygoid	Pt	—pterygoid
doppf	—dorsal opening of the pterygo-paroccipital foramen	ptf	—post-temporal fenestra
dpSq	—dorsal process of the squamosal	ptpf	—pterygo-paroccipital foramen
dvf	—dorsal venous foramen	pvfpp	—posteroventral flange of the paroccipital process
Ec	—ectopterygoid	pvpEpt	—posteroventral process of the epipterygoid
Eo	—exoccipital	pvpPro	—posteroventral process of the prootic
eopc	—external opening of the parabasal canal	qnSq	—quadrate notch of the squamosal
Ept	—epipterygoid	qpOp	—quadrate process of the opisthotic
F	—frontal	qr	—quadrate recess
fEpt	—foot of the epipterygoid	qrPt	—quadrate ramus of the pterygoid
fm	—foramen magnum	Sm	—septomaxilla
fo	—fenestra ovalis	Soc	—supraoccipital
ioc	—indentation in occipital condyle	Sq	—squamosal
Ip	—interparietal	sv	—suborbital vacuity
ipOp	—internal process of the opisthotic	T	—tabular
ipro	—incisura prootica	tpPt	—transverse process of the pterygoid
ipSq	—intermediate process of the squamosal	tso	—tuberculum spheno-occipitale
J	—jugal	V	—vomer
jf	—jugular foramen	vldfP	—ventrolateral descending flange of the parietal
jpSq	—jugal process of the squamosal	vlrPt	—ventrolateral ridge of the pterygoid
kPs	—keel of the parasphenoid	vn	—ventral notch
L	—lacrimal	vrPro	—ventral ridge of the prootic
lc	—lambdoid crest	VII	—foramen for the facial nerve (VII)
lsfo	—lateral supraoccipital fossa	XII	—foramina for the hypoglossal nerve (XII) at the mouth of the jugular foramen
M	—maxilla	BP/1	—Bernard Price Institute for Palaeontology catalogue number
mpOp	—mastoid process of the opisthotic	RC	—Rubidge collection
mpSq	—mastoid process of the squamosal	SAM	—South African Museum
N	—nasal		



6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family *Nuculanidae*

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierti* Philippi, 1861: 87.

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

*Holotype*

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

*Capital initial letters*

- (a) The Figures, Maps and Tables of the paper when referred to in the text  
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- (c) Scientific names, but not their vernacular derivatives  
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Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



J. F. DURAND

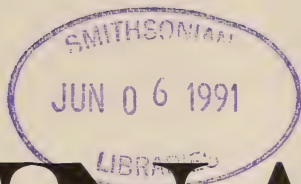
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17 (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

(continued inside back cover)



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GONDWANA

By  
JOHAN N. J. VISSER

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# GEOGRAPHY AND CLIMATOLOGY OF THE LATE CARBONIFEROUS TO JURASSIC KAROO BASIN IN SOUTH-WESTERN GONDWANA

By

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*Department of Geology, University of the Orange Free State, Bloemfontein*

(With 9 figures)

*[Paper presented at the Palaeontological Society of southern Africa Symposium, Cape Town, September 1986]*

## ABSTRACT

The major late Palaeozoic to early Mesozoic basins of south-western Gondwana were located on a platform partly surrounding a highland interior. A palaeo-Pacific Ocean formed the margin of the platform. The Karoo Basin had an oblong shape with a long axis of more than 2 000 km but, following the late Palaeozoic glaciation, it changed in size to small enclosed fluvial basins during the early Mesozoic. A migrating tectonic region, attributed to subduction of the palaeo-Pacific plate, caused the shrinking of the basin.

The climate in the Karoo Basin during the late Carboniferous varied from polar to cold. The early Permian cold stage showed distinct climatic fluctuations, resulting in glacials and interglacials, and a short-term warm period during which part of the Prince Albert Formation was deposited. Temperatures rose sharply during the late Permian and early Triassic. An abnormal cold, wet, middle Triassic resulted in the deposition of the Molteno Formation. During the late Triassic and early Jurassic, warm to warm desert conditions prevailed. Tectonically and geographically induced regional climatic patterns in the Karoo Basin were superimposed on global climatic trends. The basin was also consistently positioned at high to intermediate latitudes, suggesting that the principle of uniformitarianism cannot be applied without constraint.

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## INTRODUCTION

Knowledge on the configuration of the late Carboniferous to Jurassic Karoo Basin in space and time is absolutely necessary in understanding the distribution of lithofacies, climatic zones, and biological provinces extending beyond the domain of the southern African continent. At the present stage of our knowledge of the Palaeozoic, it is impossible to separate climatology from geography (Spjeldnaes 1981). Furthermore, sedimentation in the Karoo Basin was primarily controlled by the palaeoclimate and tectonism.



The objectives of this study are to define the position of the Karoo Basin in south-western Gondwana; to illustrate basin evolution from the late Carboniferous to the early Jurassic; to draw a macro-scale climatic curve for Karoo sedimentation; and to focus attention on anomalous climatic-geographic relationships.

For the palaeogeographic and palaeoclimatological analysis, raw data were taken from Tankard *et al.* (1982), Smith (1984), Visser (1983, 1984, 1987) and Anderson & Anderson (1985), as well as from field notes made by the author over several years of study on Karoo rocks. The palaeogeographic reconstructions are based on palaeotopographic maps, sediment dispersal patterns, thickness of stratigraphic units, depositional environments and lithofacies. In the interpretation of the palaeoclimate, use was made of palaeolatitudinal maps (Irving 1977; Smith *et al.* 1981; Hallam 1985) and the lithology of the Karoo rocks, as well as their fossil content. Although maps based on palaeomagnetic evidence suffer from considerable uncertainties in areas where reliable determinations are scarce, the apparent polar wander curve for the late Carboniferous to Jurassic shows a fairly consistent trend from various sources of literature.

A modified Gondwana reconstruction, based on one by Norton & Sclater (1979), was used for south-western Gondwana. In this reconstruction the Falkland Islands were considered as part of a rotated microplate and were repositioned alongside the Transkei coast of southern Africa to achieve a better fit for the palaeomagnetism, geology and palaeontology between the two regions (Mitchell *et al.* 1986; Visser 1987). In the palaeoclimatic reconstruction a provisional stratigraphic time scale for the Karoo Sequence, based on fossil evidence, depositional rates and isotopic age determinations, was used. However, more refined age data are needed, particularly for the Ecca Group above the Whitehill Formation, which forms a highly significant basin-wide climatic marker at the end of the early Permian. The age of the Dwyka Formation was partly taken from Loock & Visser (1985). The subdivision of the Palaeozoic and Mesozoic follows that of Harland *et al.* (1982), except for the Triassic where an informal subdivision of 'early', 'middle' and 'late', based on climatic trends, is used.

## PALAEOGEOGRAPHY

### *Karoo Basin in south-western Gondwana*

To understand the tectonic evolution of the Karoo Basin, it is essential to briefly refer to the regional geography of south-western Gondwana during the late Palaeozoic. This part of Gondwana consisted of southern South America, southern Africa, Falkland Islands, East Antarctica, and other microplates in West Antarctica (cf. Storey *et al.* 1988), as well as inundated microplates in the southern Atlantic Ocean (Fig. 1).

South-western Gondwana consisted of an elevated continental interior (e.g. Transvaal and Windhoek highlands) with trough-faulted, intracratonic basins

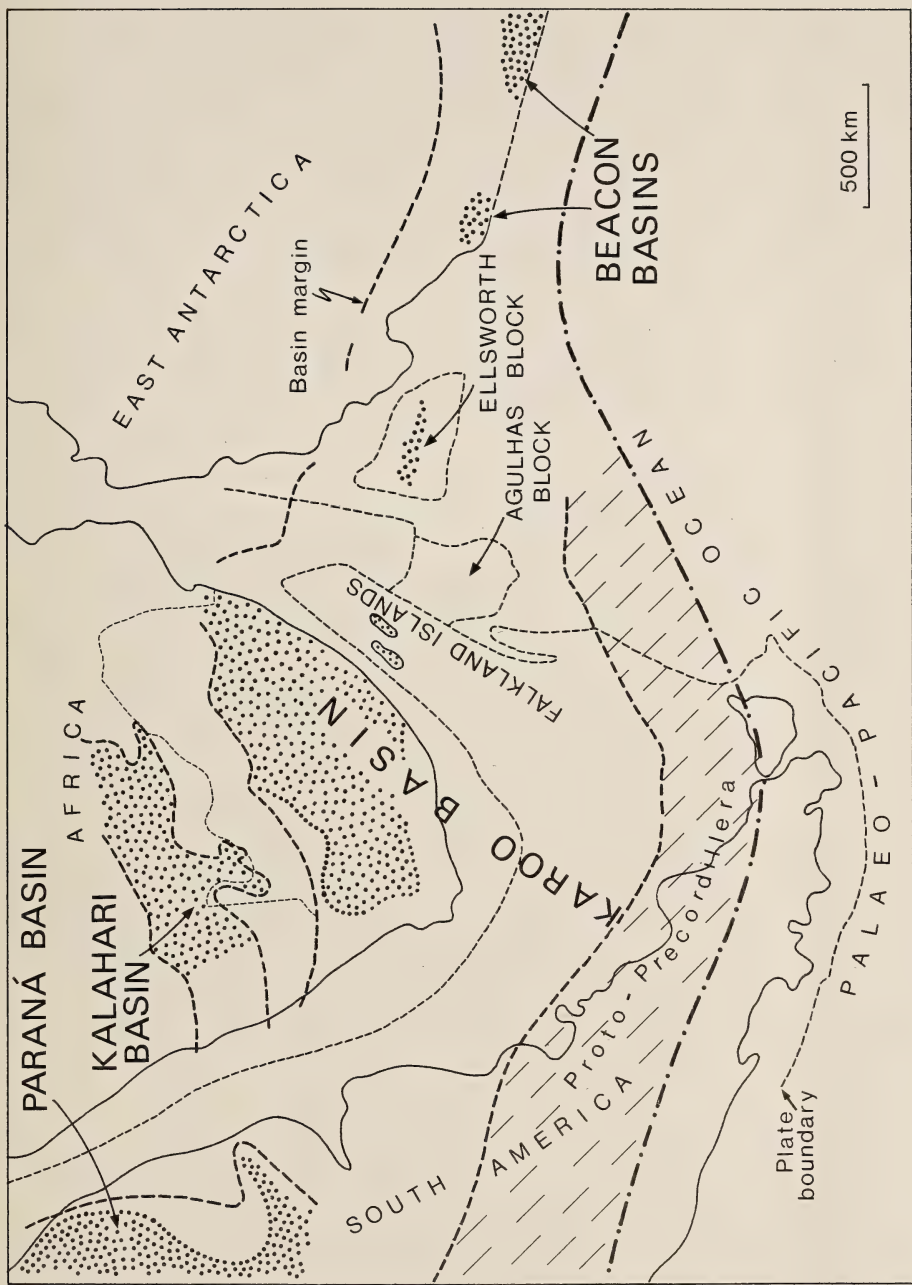


Fig. 1. The Karoo and other basins in south-western Gondwana during the late Palaeozoic. Gondwana reconstruction modified after Norton & Sclater (1979).

(e.g. Kalahari Basin). Southwards the uplands merged into a broad platform region on which the major depositional basins (e.g. Paraná, Karoo and Beacon basins) were located. A prominent mountain belt (proto-Precordillera), formed by the continued subduction of the oceanic palaeo-Pacific plate below the Gondwana plate since the Devonian or early Carboniferous, separated the platform region from the palaeo-Pacific Ocean (Lock 1980; Smellie 1981; Forsythe 1982). As a result of possible underplating (cf. Park 1988), this tectonic zone migrated northwards during the late Palaeozoic and early Mesozoic, until it reached the present southern Cape.

#### *Glaciated Dwyka Basin*

Very little is known about the pre-Dwyka landscape, as a non-depositional period of at least 30 Ma (end of Visean to the end of the Westphalian) preceded

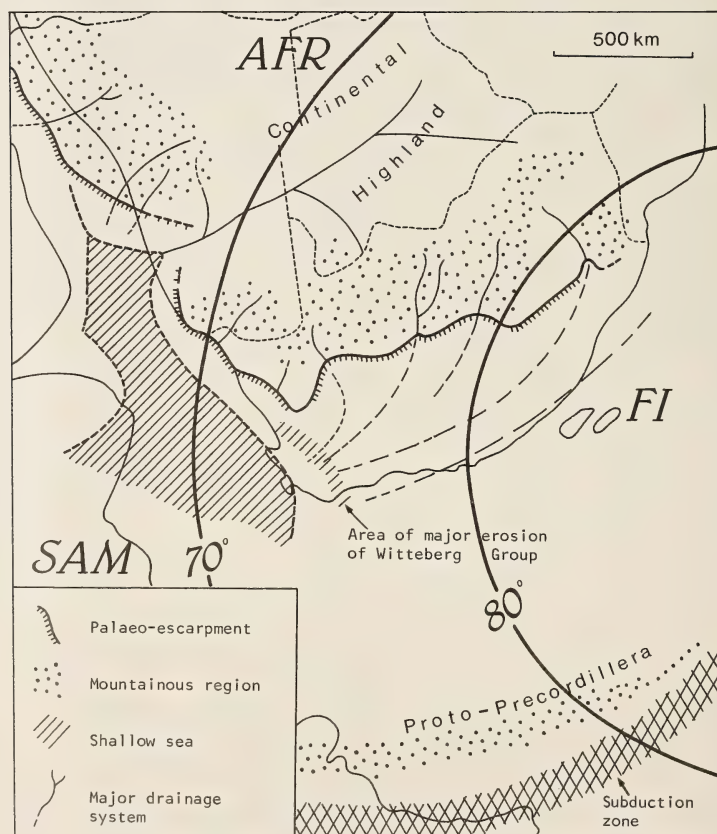


Fig. 2. Pre-Karoo (late Carboniferous) geography (after Visser 1987). Palaeolatitudes (at  $\pm 310$  Ma) after Smith *et al.* (1981). AFR = Africa, SAM = South America, FI = Falkland Islands.



glacial sedimentation (Loock & Visser 1985). Continental uplands dissected by a major river system, the later Kalahari Basin, and a fairly flat-lying basinal plain in the south were probably the major morphological elements (Fig. 2). Sea-level was low as a result of the global Namurian regression (cf. Veevers & Powell 1987) and in the south-western corner of the Karoo Basin, up to 200 m of lower Carboniferous Witteberg strata were eroded from the plain's surface (Visser & Loock 1982). Drainage was westwards into a shallow sea arm, which can be attributed to abortive rifting of this part of south-western Gondwana.

The Dwyka Basin, during maximum glaciation, consisted of an elongated (>2 000 km) east-west depository extending into Antarctica (Fig. 3). It was bounded on the north by highlands, extending from East Antarctica across southern Africa to South America, and on the south by an alpine-type mountain range (proto-Precordillera). The northern mountainous plateau probably attained elevations of 2 000 to 3 000 m, whereas the alpine-type mountains were about 1 500 m above sea-level (Martin 1981; Visser 1987). A palaeo-escarpment, up to 400 m high, separated the northern highlands from the basin in the south. The subsidiary intracratonic Kalahari Basin was fault controlled.

Both basin and highlands were completely ice covered for most of the time, but the western sea arm probably only had a sea-ice cover during winter. During two interglacials this sea transgressed eastwards, almost up to the Falkland Islands.

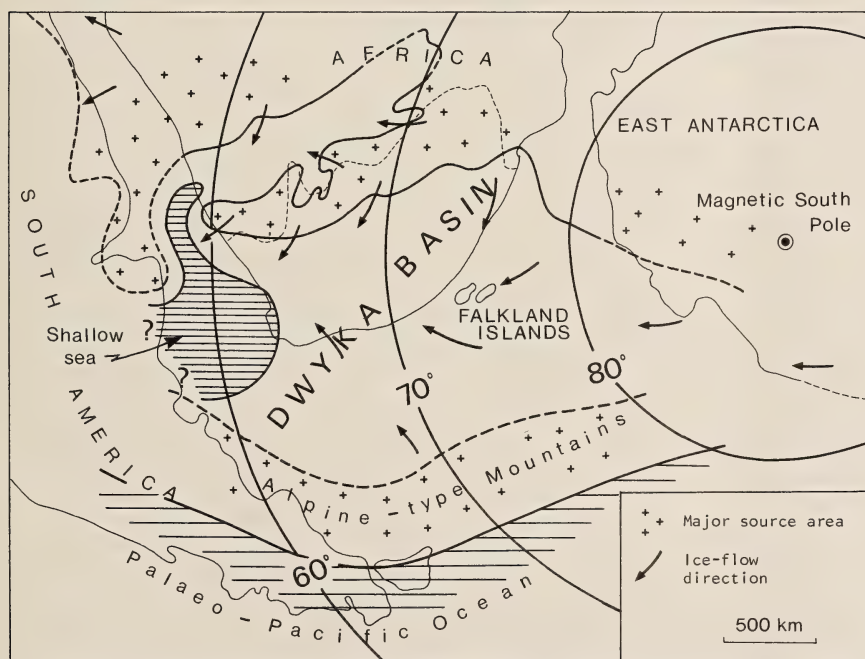


Fig. 3. The Permo-Carboniferous Dwyka basin during maximum glaciation. Palaeolatitudes (at  $\pm 290$  Ma) after Smith *et al.* (1981).

Islands, along the basin axis that was isostatically depressed by the weight of the ice as well as accumulated glacial debris. At the beginning, ice flow into the basin was mainly from the north and south. Where the ice flowed over bedrock, its thickness at the basin centre was probably in the order of 4 000 m but later, when the ice advanced over diamicton, its thickness decreased to about 1 000 m. Ice thickness over the northern highlands at maximum glaciation varied from about 2 600 to 3 000 m (Visser 1987).

The early Permian post-glacial basin shows rapidly changing geography (Fig. 4). After ice retreat only small local ice caps remained on the highest mountains. The inundation of large parts of south-western Gondwana can be attributed to a combination of sea-level rise (Stavrakis (1986) suggested a rise of 100 to 150 m on deglaciation) and isostatic depression. Although post-glacial rebound took place, the depth of isostatic subsidence was such that this uplift did not elevate the sediment-water interface above sea-level.

The Irati Sea, which covered the Paraná Basin, was in continuity with the Whitehill sea in the Karoo Basin (Oelofsen 1981). An eastern limit for the Whitehill sea is defined by the absence of black shales on East Falkland (pre-

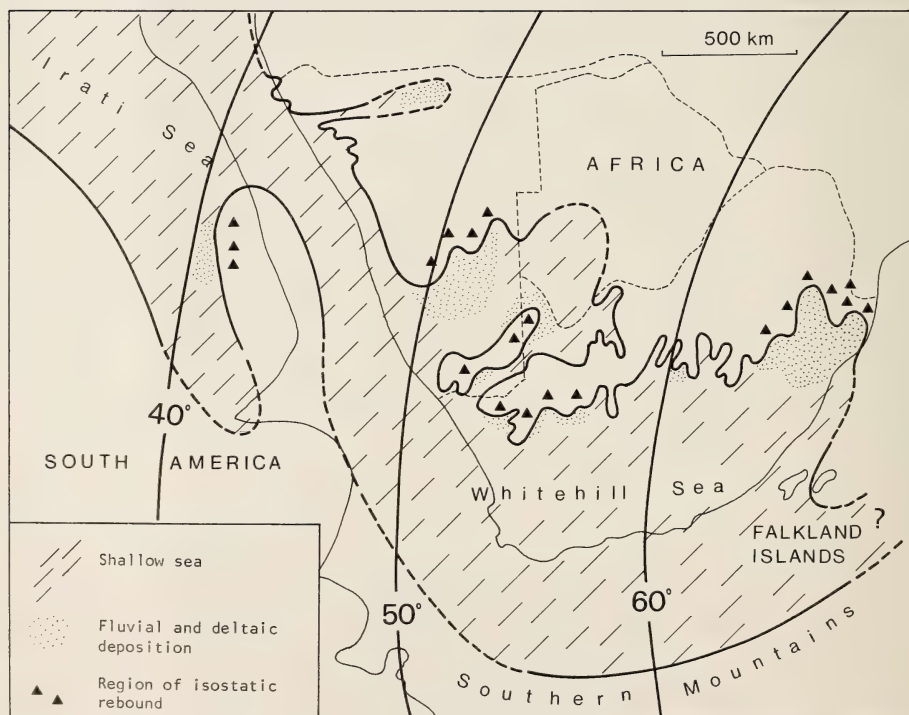


Fig. 4. Post-glaciation ( $\pm 260$  Ma) palaeogeography of the Karoo Basin and surrounding areas. Shoreline of the Irati and Whitehill seas modified after Oelofsen (1981). Palaeolatitudes after Smith *et al.* (1981).

rotation and drift), but the original extent of the sea to the south-west is unknown. The shallow seas had a typical fjord coastline in the north, whereas in the south uplift along the proto-Precordillera caused northward regression of shorelines, especially in South America. Water conditions ranged from fresh through brackish to normal marine, depending on the rate of meltwater inflow from the mountains. Isostatic rebound along sections of the northern highlands caused extensive erosion of the glacial deposits and basement rocks. Debris was deposited as deltaic and fluvial beds in fjord heads and shallow embayments (Fig. 4) that were favourable for coal formation (Falcon 1986).

### *Epicontinental Ecce Basin*

The large marine to non-marine basin formed a transition from an open shelf to an enclosed basin with major source areas in the south, west and north

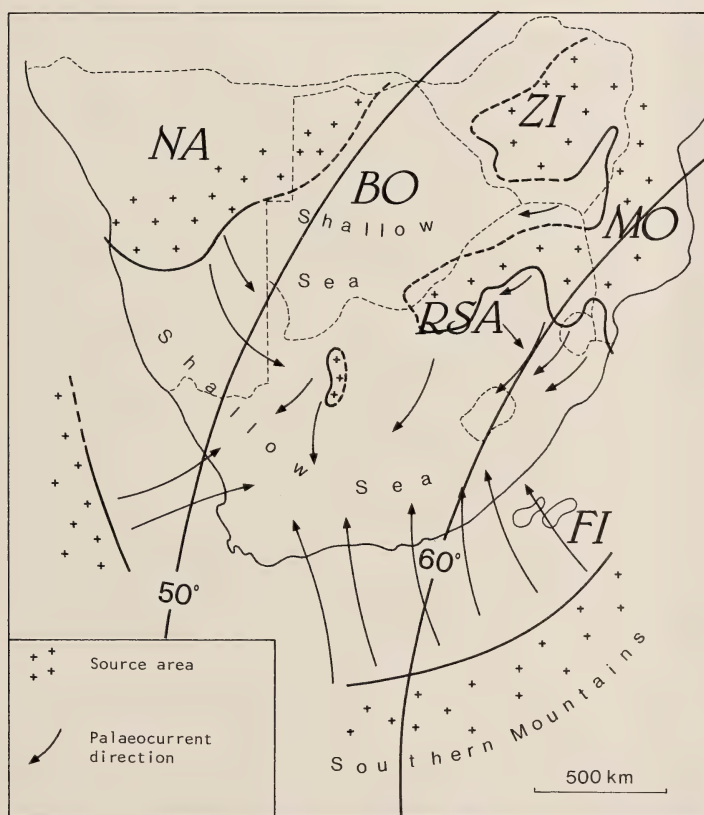


Fig. 5. The later Permian Ecce basin. Palaeolatitudes (at  $\pm 255$  Ma) after Smith *et al.* (1981). NA = Namibia, BO = Botswana, ZI = Zimbabwe, MO = Mozambique, FI = Falkland Islands, RSA = South Africa.



(Fig. 5). Subsidence of part of the northern highlands led to large-scale inundation of the region. Water depths in the south were up to 700 m (Kingsley 1981), although it was much shallower in the north. The bottom sediments consisted mostly of black mud. The presence of abundant pyrite in the black shale is also suggestive of highly reducing benthic conditions, probably well above the water-sediment interface. Such a soft muddy bottom with toxic conditions would have been unfavourable to a benthic fauna and, if such conditions were associated with a low pH, the destruction of all organisms settling on the bottom after death would have occurred. This could account for the scarcity of body fossils in these rocks.

A new development in the basin evolution was the appearance of a source area in the west that may be attributed to uplift caused by hot spot migration (cf. Anderson 1982) preceding the break-up of Gondwana. The prominent southern mountains, located a few hundreds of kilometres from the present outcrop area of the Ecca Group, consisted of low-grade metamorphic rocks

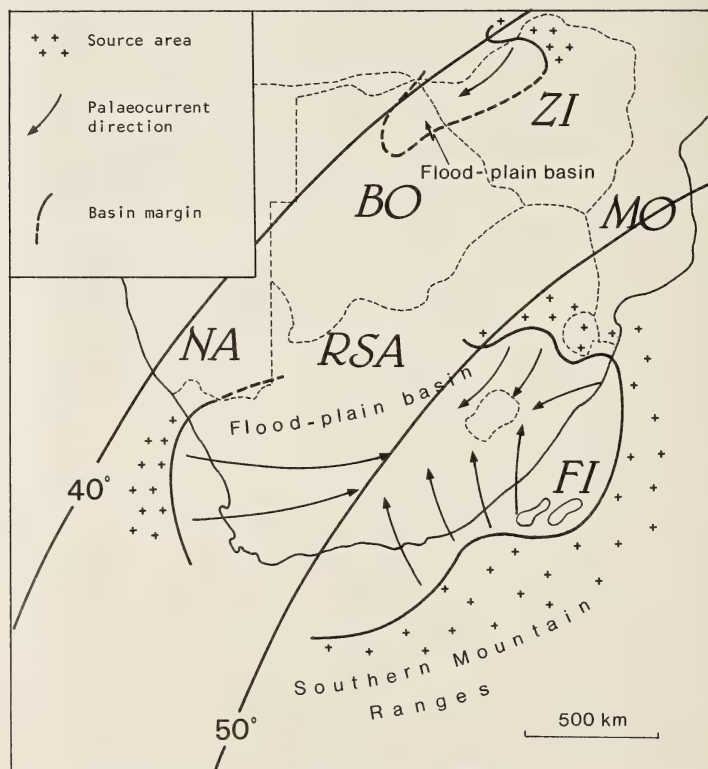


Fig. 6. Early Triassic intracratonic Beaufort basins. Palaeolatitudes (at  $\pm 245$  Ma) after Smith *et al.* (1981). NA = Namibia, BO = Botswana, ZI = Zimbabwe, MO = Mozambique, RSA = South Africa, FI = Falkland Islands.

associated with synorogenic intrusive and extrusive magmatic activity (Elliot & Watts 1974; Kingsley 1981).

#### *Intracratonic Beaufort basins*

During the Triassic, south-western Gondwana underwent a dramatic change in basin evolution with the formation of enclosed intracratonic basins. In addition to the major Karoo Basin in the south, a much smaller one developed in northern Zimbabwe (Fig. 6). The true extent of the basins will never be known, except where prominent highlands defined their margins. These fluvial basins had a largely centripetal drainage but the size of the rivers depositing the widespread flood-plain muds and silts suggests there must have been a basin outflow, probably towards the north-west and west (Botswana and northern Namibia?), where the most distal fluvial facies were deposited. However, these sediments are not fully preserved, as they were probably removed by uplift and erosion during the pre-Stormberg hiatus.

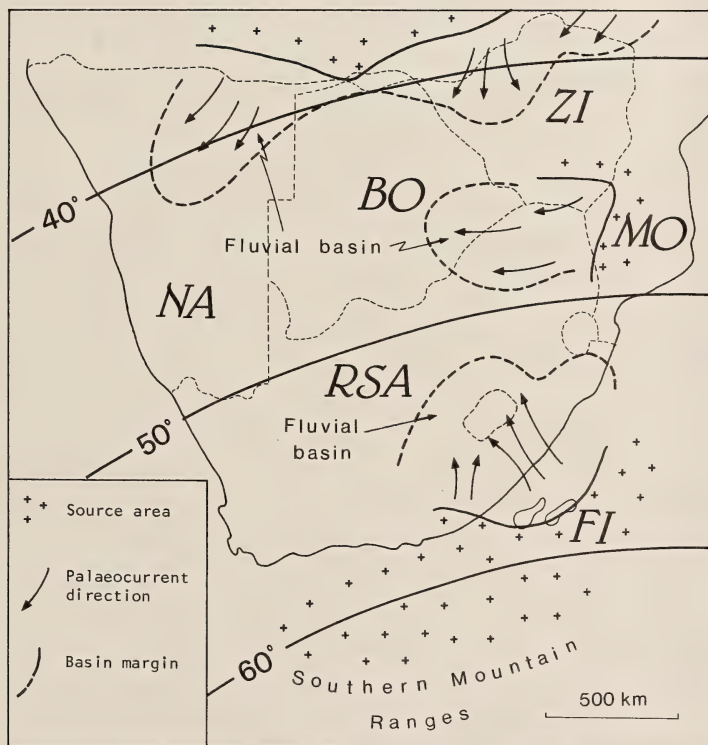


Fig. 7. Middle to late Triassic fluvial Stormberg basins. Palaeolatitudes (at  $\pm 225$  Ma) after Smith *et al.* (1981). NA = Namibia, BO = Botswana, ZI = Zimbabwe, MO = Moçambique, RSA = South Africa, FI = Falkland Islands.

Plate tectonics in the far south greatly influenced the palaeogeography. Crustal deformation and uplift migrated northwards so that during Beaufort deposition prominent mountain ranges were then located close to the present southern African coastline. Crustal uplift in the west also resulted in basinward migration of source areas.

#### *Fluvial Stormberg\* basins*

An erosional period of up to 10 Ma separated the fluvial Stormberg sedimentation from the underlying Beaufort beds in the south. During this period large areas were probably stripped of their Beaufort sediment cover. The Stormberg beds were deposited in small isolated fault-controlled basins (Fig. 7) with mountainous sources located mostly in the south-east, east and north. Typical

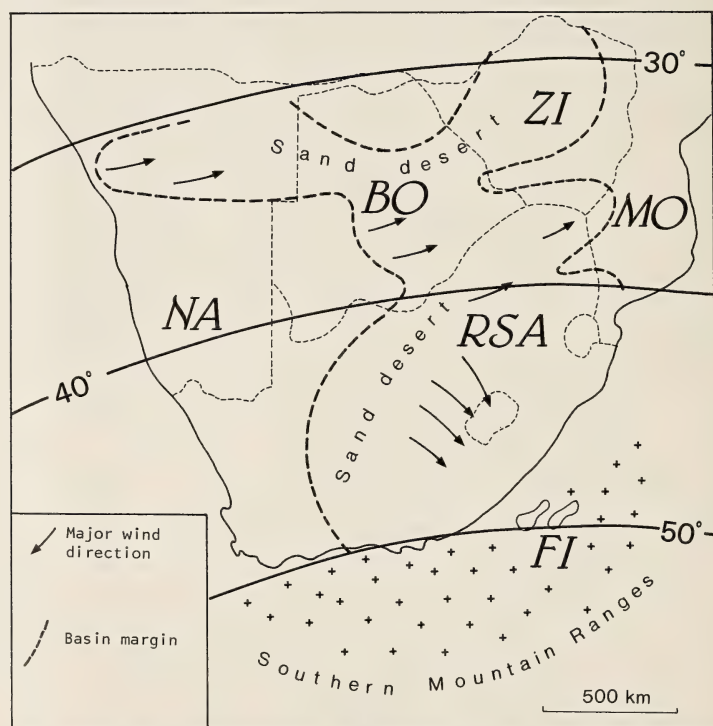


Fig. 8. The early Jurassic aeolian Stormberg Basin. Palaeolatitudes (at  $\pm 205$  Ma) after Smith *et al.* (1981). NA = Namibia, BO = Botswana, ZI = Zimbabwe, MO = Mozambique, RSA = South Africa, FI = Falkland Islands.

\* The term 'Stormberg' is informally used for the combined Molteno, Elliot and Clarens formations.



thick clastic wedges accumulated at depocentres that showed a progressive shift towards the east and north (Visser 1984). The noticeable absence of deposition in the west may be attributed to those regions preceding break-up of Gondwana.

The mountainous sources in the south-east had an elevation of up to 4 000 m (Turner 1975) and were initially drained by predominantly braided streams during deposition of the Molteno Formation and by meandering streams at a later stage. The distal fluvial facies of these stream systems probably accumulated in Okavango-type swamps in the west (Visser 1984).

#### *Aeolian Stormberg Basin*

During the early Jurassic, fluvial sedimentation was largely replaced by aeolian deposition over a large part of south-western Gondwana, as a result of a climatic change (Fig. 8). The lateral extent of the aeolian basin margin is highly speculative, as deposition was independent of the palaeoslope. Westerly winds reworked and transported the unlithified fluvial sediments (including the distal facies) of the Stormberg basins (Visser 1984). The highlands in the south-east, east and north formed a barrier to the transportation of sand and airborne silt. This resulted in thick accumulations of sediment on the windward side of the uplands.

### PALAEOCLIMATOLOGY

Climatology is the net result of a number of integrated parameters (admission of solar energy, atmospheric composition, configuration of landforms and ocean basins, sea-level, pole position, and oceanic and atmospheric circulation), the relative importance of which we do not yet fully understand. In the discussion of late Palaeozoic and early Mesozoic climates, reference will be made to some of these parameters, although those of extraterrestrial origin are not dealt with. Furthermore, to simplify discussion, only polar, cold, temperate, warm and warm desert climatic zones are referred to.

#### *Carboniferous*

Globally the early Carboniferous (320–360 Ma) had a warm climate with small latitudinal gradients (Frakes 1979; Boucot & Gray 1982). No Karoo rocks of this age were preserved and the upper part of the Witteberg Group thus constitutes the only source of evidence for reconstructing the pre-Karoo climatology, which appears to have been cool to cold (pers. comm. J. C. Looek; Fig. 9). This conclusion is substantiated by a palaeolatitude of  $>60^{\circ}\text{S}$  for the region (Smith *et al.* 1981). Although global temperatures were apparently high during the early Carboniferous, the proximity of the basin to the south pole and the location of the pole largely over land, resulted in the anomalous climate of this region. As suggested by Spjeldnaes (1981), it is suspected that the cold climate was confined to a narrow zone around the pole during globally warmer periods.

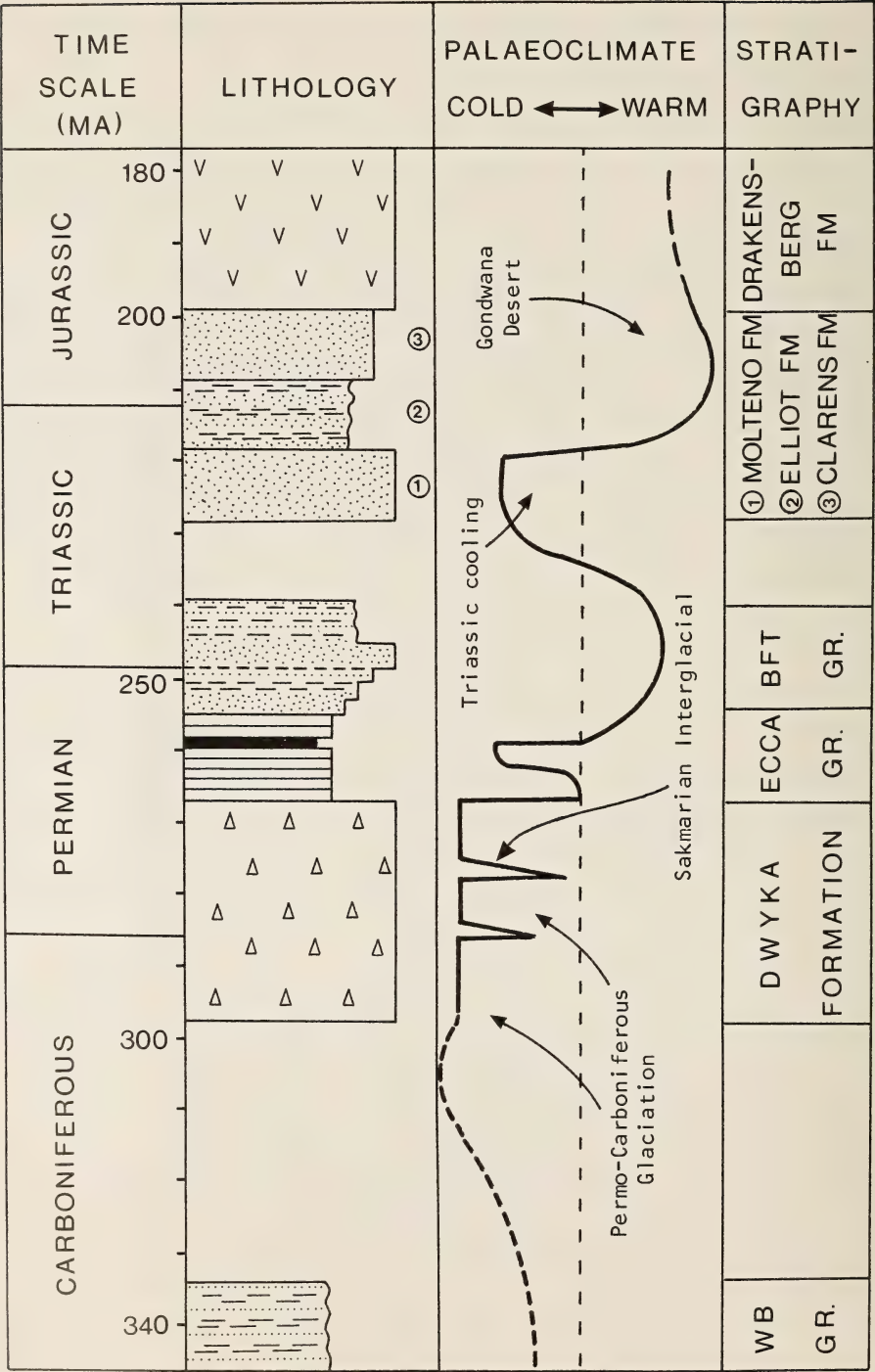


Fig. 9. The middle Carboniferous to early Jurassic climatology of the Karoo Basin.

Global temperatures dropped during the late Carboniferous (286–320 Ma) and the climate became cool and humid (Frakes 1979). Although there was a period of non-deposition in the Karoo Basin during the late Carboniferous that precludes climatological interpretation, some facts suggest the presence of a polar to cold climate (Fig. 9). Pre-Dwyka palaeosols are noticeably absent, rock fragments at the base of glacial deposits indicate blocky weathering and, on parts of the basinal plain, very little erosion took place during the hiatus. These phenomena suggest the existence of dry polar conditions without sufficient moisture for major ice cap formation over the Karoo Basin and adjoining areas. The location of the Karoo Basin at latitude 70° to 80°S and unfavourable atmospheric circulation patterns (polar easterlies blowing over a vast interior plateau) support such a climatic interpretation.

The duration of polar conditions is a matter of contention. Glacial sediments of Oligocene age (31 Ma) are preserved at McMurdo Sound, Antarctica, and give an indication of the age of the Cainozoic glaciation (Harwood 1986). By about 15 Ma ago the Antarctic Ice Sheet was well established and reached its maximum about 6.5 Ma when its effects were recorded in southern South America (Tyson 1986; Van Zinderen Bakker & Mercer 1986). South-western Gondwana probably had its total maximum ice cover between the end of the Westphalian and the Permo–Carboniferous boundary. If the 25 Ma period of the Antarctic Ice Sheet build-up is used as a standard, then the onset of regional polar conditions in south-western Gondwana could have occurred between 310 and 320 Ma (Fig. 9). At least during the lower part of the Namurian ( $\pm 12$  Ma), the Karoo Basin and surrounding area were thus completely ice free, but subjected to cold-climate weathering.

During the latest Carboniferous (Stephanian) when the Karoo Basin was situated between latitudes 60° and 75°S (Fig. 3), extensive deposition of glacial debris occurred. The diamictites and associated rock types are suggestive of a temperate to subpolar glaciation. At that stage the pole was located over Antarctica and the large continental ice mass resulted in overall stronger air circulation patterns. Strong westerlies thus supplied abundant moisture maintaining an extensive ice cover.

### *Permian*

Globally the lower third of the Permian is considered to have been cold, whereas the upper two thirds were temperate to relatively warm (Frakes 1979; Hallam 1985). The early Permian (Asselian–Kungurian; 258–286 Ma) climate in the Karoo Basin was very unstable, with alternating cold and temperate stages. Glaciation continued for most of the time but the main ice thrust into the basin was from the east at this stage, when the ice cap was situated over Antarctica. As the basin was located at the unstable margin of the ice sheet, well-developed interglacials are recognized (Fig. 9). Although the area lay between latitudes 50° and 65°S (Fig. 4), the large Antarctic ice mass still had a profound effect on circulation patterns in the Southern Hemisphere. The abundance of dropstone



argillite and the presence of wood fragments, together with a variety of fossils in the interglacial beds, suggest cold water and the existence of subarctic woodlands.

The Prince Albert Formation was deposited during one of these short-term warmer periods, but overall the climate was cold and wet (Fig. 9). Microflora from the coal-bearing strata indicate fluctuating cool-cold temperatures with cool temperate woodlands on exposed land areas (Falcon 1986). During this stage a small ice cap could have been maintained over the highlands. Cool conditions also prevailed during deposition of the lower part of the Whitehill Formation, but then a dramatic climatic change to higher temperatures took place (Fig. 9). Water temperatures rose sufficiently for reptiles (*Mesosaurus*) to invade the Irati and Whitehill seas (Oelofsen 1981). Suitable explanations for these short-term climatic fluctuations (third order Vail cycles) during the early Permian are not yet available. It might be that global climate ameliorated in a pulsating manner after the extensive Permo-Carboniferous glaciation.

The late Permian (Ufimian-Tatarian; 248–258 Ma) climate was warm and seasonal with a savanna-type plant cover in the basin (Falcon 1986; Fig. 9). This conclusion is substantiated by the appearance of reptiles on land, annual growth rings in trees, and the presence of reddish palaeosols with calcrete nodules in the lower Beaufort Group. At this stage the basin was situated between latitudes 50° and 60°S and anticlockwise rotation of south-western Gondwana (strike of the palaeo-Pacific margin changed from north-south to north-north-west to south-south-west) probably accelerated the climatic change from cold to warm.

### *Triassic*

Globally the Triassic climate was warm and probably seasonal, with atmospheric circulation sluggish in the absence of polar ice caps (Hallam 1985). In the Karoo Basin the early Triassic (Anisian and Ladinian; 231–248 Ma) climate was also warm and very similar to that of the late Permian, except that it was perhaps more equable (Tyson 1986). The basin was situated between latitudes 45° and 55°S (Fig. 6). At this stage the magnetic south pole was located over the palaeo-Pacific ocean, and the orientation of the palaeo-Pacific margin of south-western Gondwana changed from north-north-west to north-west. This caused a partial obstruction of the flow of cold water towards the equator, which in turn would have restricted the width of the cold circum-polar zone.

The apparent cold climate in the Karoo Basin during the middle Triassic (Norian and Carnian; 219–231 Ma) was anomalous to the global pattern. A sudden appearance of *Dicroidium* flora, an absence of red palaeosols and reptilian fauna, and the change in fluvial systems during the deposition of the Moltano Formation, suggest dramatic climatic changes. Unfortunately, the formation unconformably overlies the Beaufort Group with a hiatus of about 10 Ma (Fig. 9). This prevents the recognition of any transition from a warm early to a cold middle Triassic.

This dramatic drop in temperature is attributed to a change in tectonic style of the Karoo Basin (small fault-controlled basins), severe uplift in certain

regions, and a rapid basinward displacement of the south pole (cf. Smith *et al.* 1981). Turner (1975) suggested that the southern mountain ranges, which were situated at latitude 60°S, could have maintained small ice caps during this cold and wet stage, which was, however, of very limited duration.

The late Triassic (Rhaetian; 213–219 Ma) was warm and dry. This is suggested by the return of a reptilian fauna and the formation of reddish palaeosols with calcrete nodules (Fig. 9). Climatic conditions were very similar to those of the late Permian. The contact between the Molteno and Elliot formations is transitional and implies a gradual change from a cold to a warm climate. However, the interbedded coarse-grained sandstones near the base of the Elliot Formation, which are identical to those of the Molteno Formation, are suggestive of a change in temperature rather than a decrease in rainfall during the beginning of the Elliot sedimentation.

### *Jurassic*

Global climate during the Jurassic was warm and dry (Frakes 1979). This conclusion is substantiated by the warm desert conditions prevalent in the early Jurassic Karoo Basin (Fig. 9). The aeolian sandstones, flash-flood deposits and greenish playa lake mudstones also point to the extreme aridity of the region. This warm sand desert was located between latitudes 30° and 50°S (Fig. 8) and suggests that overall climatic conditions during the Jurassic must have been warmer than those of today. At this stage the strike of the palaeo-Pacific margin of south-western Gondwana had changed to almost east–west and the southern mountain ranges (part of the proto-Precordillera) obstructed moisture reaching the interior. Dry westerlies were predominantly responsible for sediment transportation in the interior desert.

Extensive volcanic eruptions started at about 200 Ma and altered the regional climate profoundly (Tyson 1986). Although conditions were still warm, rainfall probably increased considerably.

## CONCLUSIONS

The Karoo Basin experienced an evolutionary tectonic pattern as a result of plate subduction and uplift since the Devonian–Carboniferous along the palaeo-Pacific margin of south-western Gondwana. This event determined the location and altitude of the major source areas, the size of the basin, and the isolation of the fluvial basins during the Mesozoic.

Regions of locally self-induced climate profoundly influenced life and sedimentation in south-western Gondwana. These climatic anomalies can be attributed to crustal uplift, isostatic depression, proximity to ice caps, and the configuration of the land areas.

The palaeoclimatic reconstruction of the Karoo Basin shows that the principle of uniformitarianism cannot be applied without constraint. Some of the climatic anomalies can only be explained by globally warmer or colder periods

than the present. This implies that present-day latitudinal climatic zones cannot be uniformly projected for the Palaeozoic.

### ACKNOWLEDGEMENTS

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

*Nucula largillierii* Philippi, 1861: 87.

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

*Holotype*

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

*Capital initial letters*

(a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives

e.g. Therocephalia, but therocephalian

*Punctuation* should be loose, omitting all not strictly necessary

*Reference to the author* should preferably be expressed in the third person

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'Revision of the Crustacea. Part VIII. The Amphipoda.'

*Specific name* must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

*Name of new genus or species* is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



JOHAN N. J. VISSER

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